A study of faunal succession in sheep dung

Pisolkar, Ellen

A STUDY OF FAUNAL SUCCESSION IN SHEEP DUNG

by

Ellen Pisolkar

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INTRODUCTION

The decomposition of herbivore faeces plays an important part in the recycling of nutrients within ecosystems (Fig. 1). The degree to which nutrients are cycled through this 'grazing' pathway depends on the proportion of plant production consumed by herbivores. In forest ecosystems, for example, almost all the primary production goes into the decomposer food chain, whereas on grasslands a higher fraction of primary production is consumed by herbivores (Krebs, 1978) of which about 70% is returned to the ecosystem in the form of faeces.

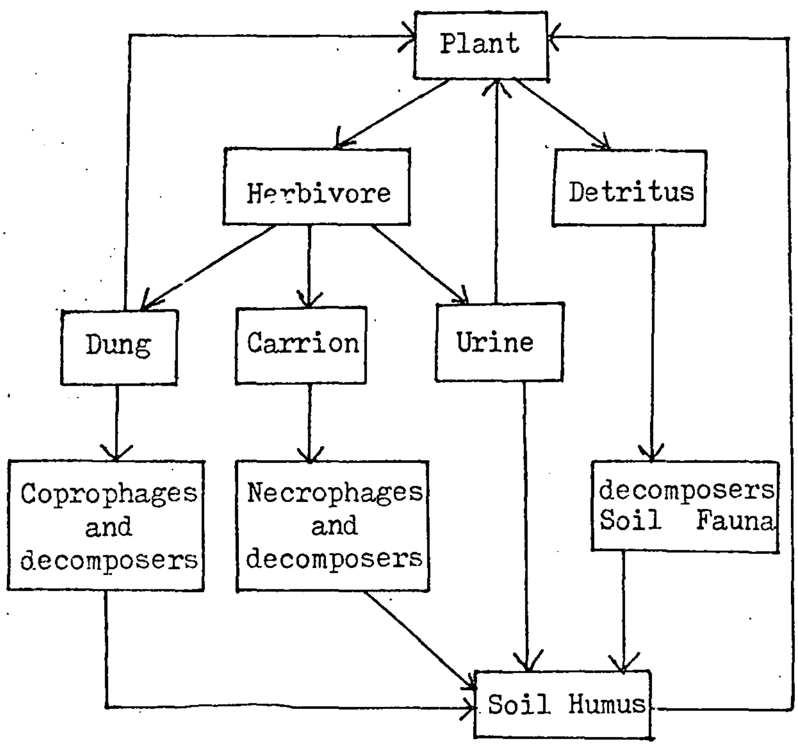


Fig. 1
Generalized Nutrient Cycle

Herbivore dung is a complex substance composed largely of water, residues of undigested herbage, products of endogenous origin and a large and varied population of micro-organisms, bacteria and coprophilous fungi and the products of their metabolism. The calorie content is high: about 4.8 kcal/gram dry weight (Olechowicz, 1974) and there is a high concentration of organic matter including protein and fat. The amount of nitrogen in dung available to plants is higher than in leaf litter and the low carbon to nitrogen ratio is generally thought to encourage decomposition by enhancing the metabolic efficiency of bacteria and fungi (Garrett, 1963, quoted in Angel and Wicklow, 1974).

The disappearance and decomposition of dung follows three major pathways (Denholm-Young, 1979). Firstly, it can be transported into the soil through the action of rain leaching the dung, worms transporting particles into the soil, dung-burying dung-beetles, e.g. Geotrupes spp. and through the death and pupal cases of soil-pupating insects that have fed and grown in the dung, e.g. Aphodius rufipes (L.). Secondly, it can disappear in gaseous form through the metabolism of bacteria, fungi, protozoa, alga and invertebrates which then release NH_4, CO_2 and other waste gases. Thirdly, the dung can be assimilated into the tissues of animals and fungi and exported in their bodies or through fungal spores.

There are many variables affecting the relative importance of each of these pathways in the decomposition of droppings, including geographic location, the surrounding vegetation, size of dung, weather, season.

Invertebrates contribute to the decomposition of dung by eating the dung and exporting material in their bodies, by releasing gaseous waste products resulting from this metabolism and by transporting particles of dung into the soil. In addition, invertebrates can have a stimulative effect on the action of bacteria and this is possibly their most important role in decomposition (Holter, 1979; Denholm-Young, 1979; Breymeyer, 1974).

Even at high densities coprophagous adults and larvae assimilate only a small fraction of the energy available. However, the high ingestion rate resulting from a low assimilation efficiency (Holter, 1979) results in a large amount of material passing through the invertebrate guts. Holter (1975) investigated dung beetle larvae (Aphodius rufipes) in cow pats and calculated that about 36% of the cow pat passed through the larval gut at least once, although only 1.8-3.8% was assimilated. Thus, invertebrates may contribute considerably to dung decomposition by the indirect effects of stimulating microbial decomposition and encouraging the physical disintegration of the dung through their movements.

The insect species associated with dung are fairly well documented (Hafez, 1939; Valiela, 1969b). Studies have concentrated on various aspects of dung fauna, for example, investigations of fly larvae populations have been carried out to gain an insight into the habits of fly pests breeding in dung (Papp, 1976; Valiela, 1969a; Greenham, 1972). There have also been several autecological studies on various flies and beetles (Gibbons, 1968; White, 1957; Landin, 1961) and a number of studies concerned with the value in agricultural terms of dung-burying beetles (e.g. Geotrupes spp.) with a view to their possible introduction into Australia (Bournemissza and Williams, 1970; Gillard, 1967). 9

Several investigations have approached the study of dung fauna by considering a dropping to be an ecological unit with the associated species comprising a community. Changes in the species composition of this community would then be regarded as succession. Mohr (1943) gave semi-quantitative data on the surface and internal succession of cattle dung during the first five days of age. Laurence (1954) investigated the larval inhabitants of cow pats in terms of seasonal change and successional change with pat ageing. However, the pats were not sampled in a systematic and quantitative manner with regard to ageing and no detailed information on changes in the relative numbers of species was given.

Papp (1976) studied dipteran larval succession in cow pats and suggested that the coprophages fell into two main categories with regard to feeding and development: primary larvae and secondary larvae, found earlier and later in the ageing of dung.

Recent workers have provided quantitative information on the dung fauna as part of a detailed investigation of a particular ecosystem (Olechowicz, 1974; Kajak, 1974; Breymeyer, 1974) or as part of a study of the components of decomposition (Nakamura, 1975; Denholm-Young, 1979).

Recent detailed analyses of succession and diversity in the beetle community of cow pats (Hanski and Koskela, 1977; Hanski and Koskela, 1978) illustrate the way in which this ecological unit lends itself to quantitative study on associated sections of the community.

Few workers have investigated invertebrate communities in droppings other than cow pats. Olechowicz (1974) is a notable exception. She studied faunal succession in sheep droppings. However, due to 'lumping' of data, especially in terms of the beetle fauna, details of changes in numbers and the species involved are not evident.

In addition, no studies have looked at successional changes in systems that are relatively unproductive in agricultural terms and not intensively grazed or fertilized.

Thus, it was felt that a study on faunal succession in sheep droppings on upland moorland conditions would go some way towards filling this gap in our understanding of dung fauna and the variables affecting it, as well as having implications for successional changes in other communities.

Upland hill soils in Britain have a low fertility due largely to the slow rate of decomposition of accumulated organic matter resulting in a slow recycling rate of nutrients, with nitrogen and phosphorous being particularly affected (Science and Hill Farming, 1979). Thus, the production of herbage is low and only a small proportion (20 - 30%) of the production is utilized by grazing sheep (Floate, 1970), compared with 70% in a Polish upland grazing system (Olechowicz, 1974).

As about 70% of the primary production ingested by sheep returns to the ecosystem in the form of faeces, this forms an important source of available nutrients in a relatively impoverished area.

To provide information on the variables affecting faunal succession in droppings, two different vegetation types were chosen for the sample sites. These were areas dominated by grass or by heather (<u>Calluna vulgaris</u> (L.) Hull). Reconstructed sheep droppings were placed on the areas on a single day and samples were taken at intervals for a period of one month to determine faunal changes. Due to the extraction procedures used, only beetle and fly larvae, adult beetles and mites could be investigated.

In this type of experiment, where sampling is destructive, it is not possible to follow succession in one situation. The samples were put out on the same day and subsamples were taken on each sampling occasion. Therefore, the assumption made in this study is that the pattern of succession found by this method is representative of the succession taking place within each unit.

METHOD

I Site Description

(i) The Study Area

Muggleswick Common is situated in County Durham, Nat. Grid. Ref. NZ004 444 (Fig. 2). The greater part of the common lies above 300m. and contains three reservoirs. The area consists of a typical grouse-moor and is dominated by heather (*Calluna vulgaris*) interspersed with grassland areas dominated either by bracken (*Pteridium aquilinum* (L.) Kuhn), *Nardus stricta* L. or *Juncus* spp.

Soils and Geology The dominant soil group of the area is a stagnohumic gley soil including peat soils and stagnopodzols. The parent material is palaeozoic or jurassic shale and sandstone with associated drift. The parent material on the sample sites described below is a layer of sandstone.

Management of Land Areas of heather are burnt periodically to ensure a supply of food for the grouse (*Lagopus lagopus scoticus*). The area containing the sample sites is part of Waskerly Park and in common with the rest of Muggleswick common, is grazed throughout the year by Swaledale sheep, noted for their winter hardiness and ability to survive on a low nutrient diet. The density of sheep is about one per hectare. On Waskerly Park, an area of about 768 hectares, two cows and two horses were also grazed. The moor is relatively well drained with an extensive system of drainage channels.

(ii) The Sample Sites

Two sample sites were chosen as being characteristic firstly of areas dominated by heather and secondly of grassland areas (Figure 3). The areas chosen were adjacent to reduce variations resulting from aspect, topography and altitude. The sites were situated on a slope facing E.S.E., at an altitude of 442m.

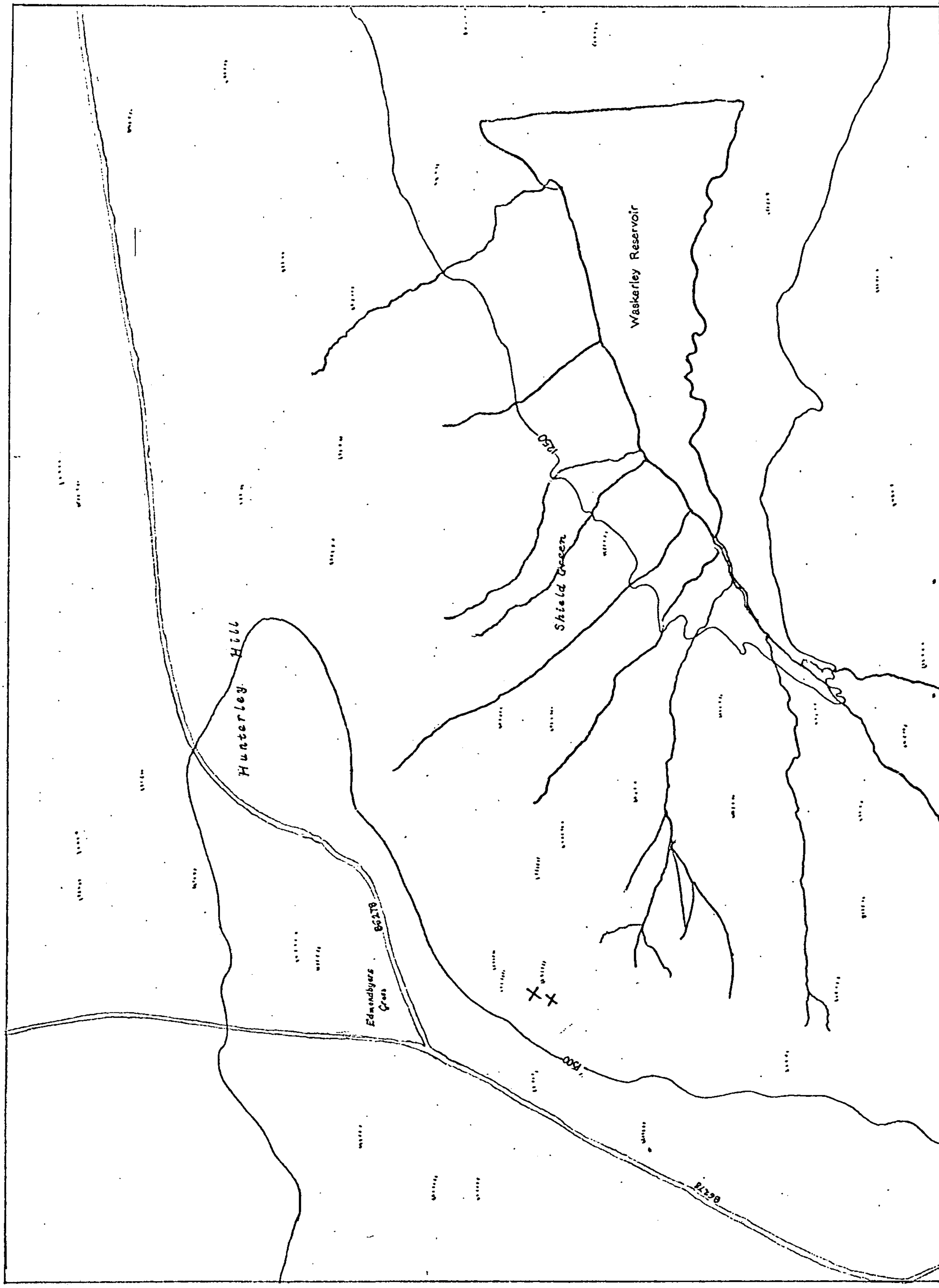
Grassland Site The depth of the peat was about 20 cm. with some deeper pockets. The plant species on this site were categorised as follows;

'dominant' - more than 60% hit on a point quadrat.
'abundant' - 20 - 60% hit on a point quadrat.
'others' - less than 20% hit on a point quadrat.

Dominant	-	*Nardus stricta* L.
Abundant	-	*Agrostis canina* L.
		Anthoxanthum odoratum L.
		Galium saxatile
Others	-	*Festuca rubra* L.
		Deschampsia flexuosa (L.) Trin.
		Juncus squarrosus
		Rhytidiadelphus squarrosus (Hedw.) Warnst.
		Mnium hornum Hedw.
		Isopterygium elegans (Hock.) Lindb.

Heather Site The peat here was shallower than on the grassland site and varied between 7 and 10 cm. in depth. The site was dominated by *Calluna vulgaris* ; about 25 cm. in height and uniform in appearance.

Figure 2 : Map of Study Area



XX - Position of Sample Sites

Grassland Site

Heather Site

Figure 3 : Photographs of Study Sites

The most abundant mosses found were;

Hypnum cupressiforme Hedw. var. ericetorum

Dicranum scoparium Hedw.

Rhytidiadelphus squarrosus

II Materials

Fresh sheep dung was collected over a period of three weeks from Muggleswick Common by walking beside the road where a high proportion of the sheep fed on the grassy areas. An attempt was made to collect only fresh dung, less than 15 minutes old. If a 'skin' had started to form, with the outer surface losing its greenish, moist appearance and turning brown, or if beetles (Aphodius spp.) had started to burrow into it, the dung was not collected. Most of the dung collected had been deposited by lactating sheep as material from lambs was not taken.

The dung was stored in plastic bags in a deep freeze until a sufficient quantity had been collected for the study. The dung collected showed great variation in terms of weight, consistency, form and percentage of dry matter. Hammer (1941) found that cow dung deposited earlier in the day had a firmer consistency than that deposited later. Dung from lactating sheep has a lower nitrogen content than dung from non-lactating sheep. The texture and nitrogen content of dung can also vary according to the type of vegetation eaten.

Thus, to ensure homogeneity of the experimental dung samples used, all the dung collected was mashed and then thoroughly mixed together. It has been found (White, 1957) that sheep dung in 'pellet' form is

Table 1: Physical and Chemical Characteristics of Dung Samples

Weight	Volume	%Dry Matter	%Moisture (100-% Dry Matter)	%Organic Matter (100-% Ash)	%Nitrogen (Kjedahl method)	Na	K	Ca	Mg
70g $\pm$ 0.8g	70c.c.	22.3% $\pm$ 0.5	77.7% $\pm$ 0.5	87.9% $\pm$ 0.4	5.46%	8.7ppm	73.1ppm	30.8ppm	13.8ppm

less attractive to certain dung fauna than droppings in a 'compact' form. The average weight of a dropping collected from the field was 68 grammes (varying from 32 to 248 g.). Therefore a sample dropping weight of 70 g. was chosen and the dung was reconstituted into samples of this size. Characteristics of the dung samples areshown in Table 1. (%Dry matter and %Organic matter were obtained as outlined in Section V, (iv) and (v) respectively).

III Design

Samples of dung were placed on each of the two study sites at 4.00 p.m. on 15 June, 1980.

On the grassland site the samples were placed 2 metres apart on a grid 32 metres by 8 metres as shown in Figure 4. Dung already present on the sampling sites was not removed.

On the heather site, the dung samples were placed according to different principles. A preliminary survey showed that dung when deposited on an area dominated by heather, was invariably found on the 'sheep paths' through the heather. These paths offered least resistance to the sheep in their progress through patches of heather.

For this reason, two sheep paths were chosen in the heather site and dung samples were placed in pairs on opposite sides of the path and 2 metres apart on one of the paths and in a single line 2 metres apart on the other path (Figure 5). To minimise destruction by sheep using the paths, the dung was placed on the side of the path rather than in the centre.

As sheep had free access to the study sites and are known for their inquisitive nature, the individual samples were not marked but were re-located using a map. Stakes were used only to mark the four corners of the grid on the grassland site and the ends of the sheep paths on the heather site.

When placed on the sites, the dung had a temperature of about 18°C. This is lower than the temperature of freshly deposited dung (38-39°C.) although this temperature falls rapidly. The dung samples, when placed on the sites, had moist outer surfaces.

Preliminary qualitative observations on reconstructed dung samples had shown that dung flies (Scatophaga spp.) and dung beetles (Aphodius spp.), usually among the first visitors to fresh dung, were immediately attracted to the experimental dung. In addition, Olechowicz (1974) found that experimental sheep dung and dung deposited directly did not differ significantly in terms of the numbers of animals colonizing it. Therefore, the same assumption was made in this study.

IV Collection of Samples

Table 2: Sampling Days, Dates and Position of Samples Collected

Age of Dung on Collection (Days)	2		4		6		8		10		16		24		30	
Date	17 June		19 June		21 June		23 June		25 June		1 July		9 July		15 July	
	G	H	G	H	G	H	G	H	G	H	G	H	G	H	G	H
Position of Dung Samples (see Figs 4 and 5)	1	1	6	6	11	11	16	16	21	21	26	26	31	46	36	36
	2	2	7	7	12	12	17	17	22	22	27	27	32	47	37	37
	3	3	8	8	13	13	18	18	23	23	28	28	35	48	40	38
	4	4	9	9	14	14	19	19	24	24	29	29	34	49	41	39
	5	5	10	10	15	15	20	20	25	25	30	30	35	50	42	40
	81	81	76	76	71	71	66	66	61	61	56	56	51	51	43	41
	82	82	77	77	72	72	67	67	62	62	57	57	52	52	46	42
	83	83	78	78	73	73	68	68	63	63	58	58	45	53	47	43
	84	84	79	79	74	74	69	69	64	64	59	59	54	54	49	44
	85	85	80	80	75	75	70	70	65	65	60	60	55	55	50	45

The dung was collected after 2, 4, 6, 10, 16, 24, 30 days. Thus, most sampling days were within the first two weeks of dung exposure, which has been found by other workers (e.g. Olechowicz, 1974) to be the period of maximal faunal change. Ten samples of dung were collected from each study site on each sampling day. The sampling days, dates and the position of the dung collected are shown in Table 2. To minimise disturbance, an everted plastic bag was quickly placed over the dung sample and the dung lifted and put in the plastic bag. To include fauna living on the dung/vegetation interface and any animal that had dropped while the dung was removed, a portion of the vegetation mat situated immediately beneath the dung was taken.

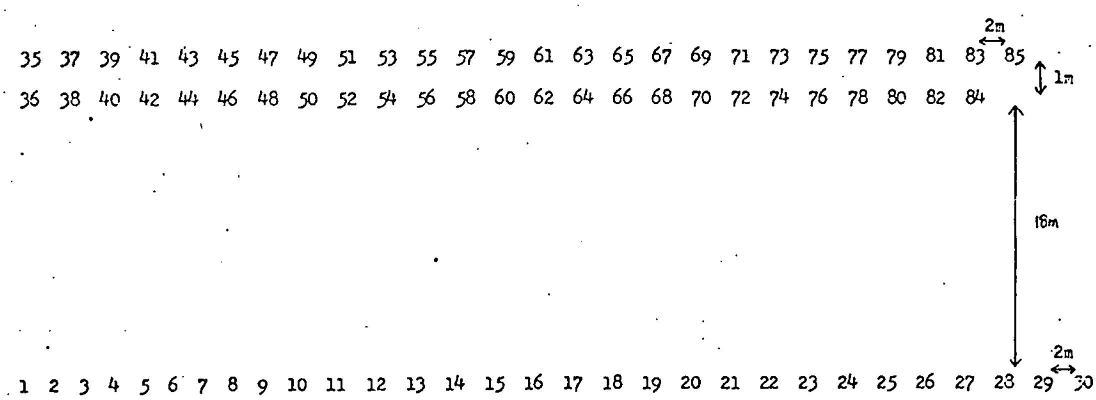
The soil below each dung sample was removed using a soil corer ($1/10m^2$) to a depth of 10 cm and each core was placed in a separate

Figure 4: Diagram to show the position of Dung Samples on the Grassland Site (Each number refers to a single dung sample)

2m ↔ (horizontal spacing); 2m ↕ (vertical spacing)

1	6	11	16	21	26	31	36	41	46	51	56	61	66	71	76	81
2	7	12	17	22	27	32	37	42	47	52	57	62	67	72	77	82
3	8	13	18	23	28	33	38	43	48	53	58	63	68	73	78	83
4	9	14	19	24	29	34	39	44	49	54	59	64	69	74	79	84
5	10	15	20	25	30	35	40	45	50	56	60	65	70	75	80	85

Figure 5: Diagram to show the position of Dung Samples on the Heather Site (Each number refers to a single dung sample)



plastic bag. On each day, five control soil cores were taken from each site.

V Extraction of Fauna and Analysis of Dung

The dung samples were extracted for fauna using a combination of hand-sorting and flotation procedures which are described in detail as follows:

(i) The degree of disintegration of the sample was noted; 1 = whole, 2 = less than 30% in pieces, 3 = 30-60% in pieces, 4 = more than 60% in pieces.

(ii) The total weight of the dung sample was determined.

(iii) About six grammes of the dung sample was removed and carefully hand-sorted for fauna using a damp paintbrush and tweezers.

(iv) This subsample, with the fauna removed was dried at 80°C for 12 hours to enable determination of the proportion of dry matter.

(v) The subsample was then ignited at 500°C for 6 hours and cooled in a dessicator before being weighed to give the proportion of ash in the dry matter. This gives an estimate of the percentage of organic matter (100 - % ash).

(vi) The remaining portion of the dung sample was hand-sorted for fauna using tweezers and a paintbrush.

(vii) The dung was then stirred into a 20% sodium chloride solution which caused the invertebrates present to float to the surface. These were removed using a paintbrush.

(viii) The fauna collected from each sample were grouped. Hydrophilidae and Staphylinidae adults and mites were killed using ethyl acetate and preserved in 70% alcohol. Most larvae were killed and stored in 70% alcohol. Some larvae were put on fresh dung in petri dishes with moist cottonwool maintaining conditions of high humidity. They were allowed to continue their life-cycle as the identification of the imagos was generally easier than that of the larvae. The Aphodius adults were kept alive in dung-filled petri dishes to await identification.

The time taken to extract fauna from 20 dung samples was at least 20 hours. Dung waiting to be extracted was stored at a temperature of 8°C. The samples from the grassland site were always processed before those from the heather site.

The main advantage of hand-sorting was the improvement of flotation extraction efficiency. Hand- sorting the dung samples reduced the size of the particles and removed many of the animals. Thus, the remaining fauna spent less time in the salt solution, resulting in a greater efficiency in the extraction of small larvae which, if remaining in the solution for longer periods of time, became immobile and difficult to distinguish from floating vegetation. Papp (1976) found 100% extraction efficiency with larvae less than 1mm. long if the numbers were fairly low. In addition, hand-sorting allowed the extraction of mites which, during the flotation process, clung to pieces of submerged fibre and could not be seen.

Soil Cores The soil cores were broken up by hand and extracted in Tullgren funnels for 2 days.

RESULTS

Ten dung samples were collected from each site on each sampling day as outlined in Method IV. However, on day 30, some samples had disappeared on the grassland site, resulting in a sample size of 8 on this site.

I. CHANGES IN PHYSICAL CHARACTERISTICS

Percentage of Dry Matter

The percentage of dry matter of the dung samples shows great variation throughout the 30 day sampling period, with similar variations on both the grassland and the heather sites (Table 3, Fig. 6). There was no clear decrease in the percentage of moisture (ie an increase in the percentage of dry matter) as has been found in studies of cow dung (Laurence, 1954; Hammer, 1941). Thus, the moisture in the dung fluctuated with rainfall and this is an indication of the porosity of the droppings. Cow pats develop a hard crust with age and this renders the dung more resistant to rewetting (Underhay and Dickinson, 1978) and to dessication (Landin, 1961).

It is conceivable that the moisture fluctuations are partly an artefact of the reconstituted dung samples. Freshly voided dung has a smooth outer surface with a thin layer of intestinal secretions. The slightly rougher surface of the experimental dung, lacking these

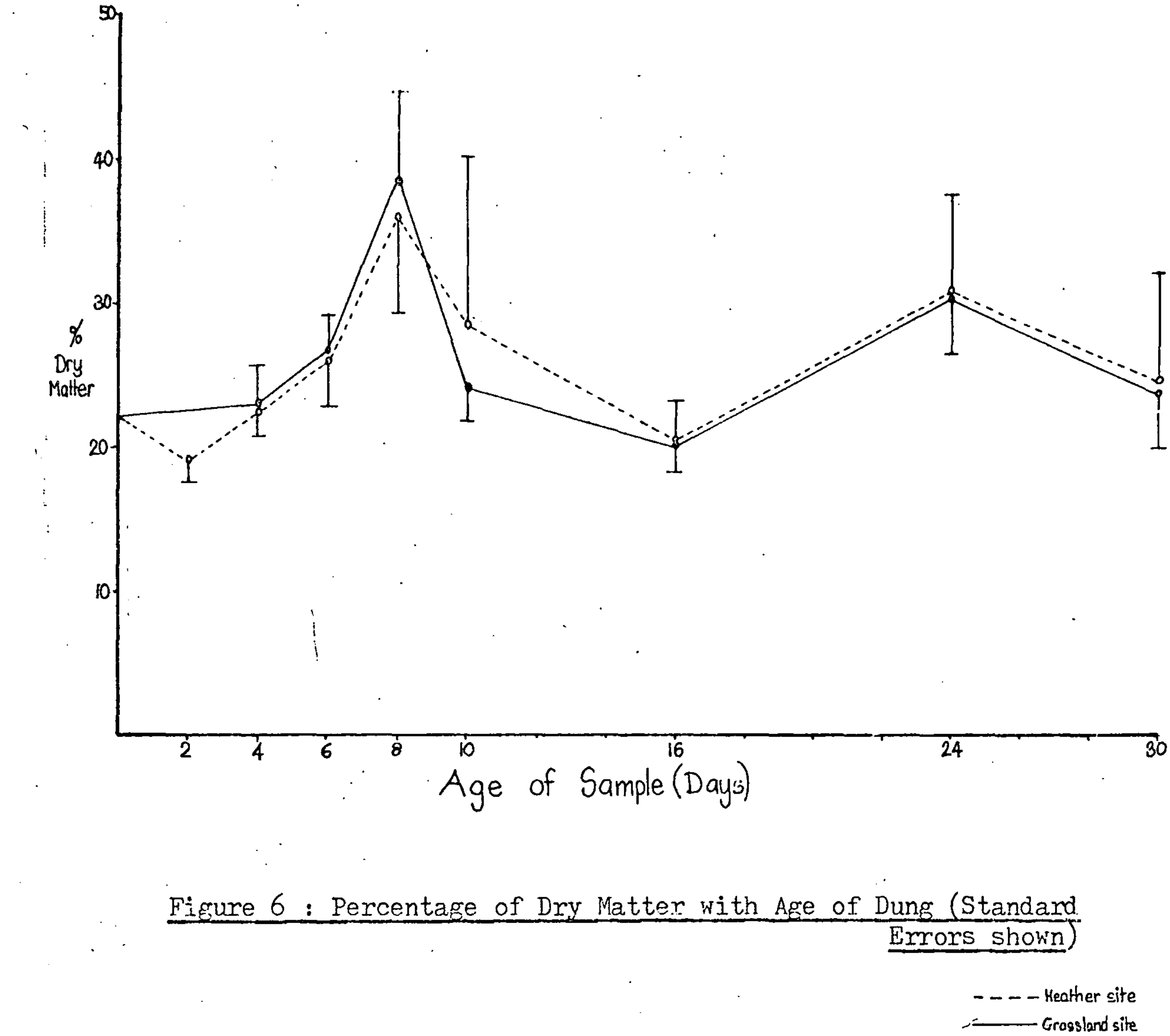


Figure 6 : Percentage of Dry Matter with Age of Dung (Standard Errors shown)

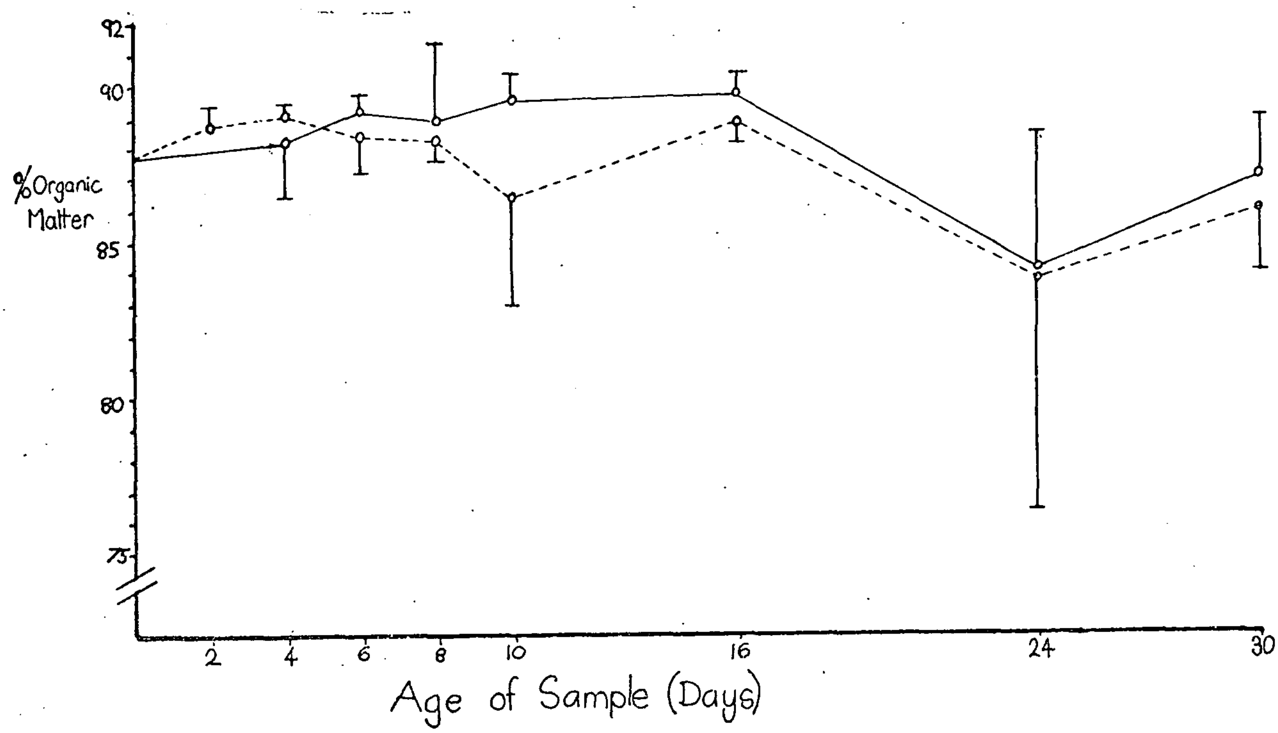


Figure 7 : Percentage of Organic Matter with Age of Dung (Standard Errors shown)

Table 3: Changes in Physical Characteristics in Dung Samples

Sampling Day	Site	% Dry Weight Mean	% Dry Weight Standard Deviation	% Organic Matter Mean	% Organic Matter Standard Deviation	Amount Dry Matter per sample (g) Mean	Amount Dry Matter per sample (g) Standard Deviation
2	Grass	-	-	-	-	-	-
	Heather	19.12	1.25	88.75	0.88	14.49	1.34
4	Grass	23.02	2.82	88.28	1.7	13.95	1.49
	Heather	22.66	1.77	89.12	0.47	14.76	0.61
6	Grass	26.81	2.33	89.24	0.52	15.48	1.61
	Heather	26.14	3.38	88.43	1.12	14.82	1.25
8	Grass	38.58	6.29	88.98	2.6	15.27	1.5
	Heather	36.05	8.68	88.28	0.54	15.08	1.32
10	Grass	24.27	2.09	89.51	0.89	14.18	0.63
	Heather	28.53	11.7	86.39	3.33	14.03	1.70
16	Grass	20.14	1.7	89.83	0.58	12.75	0.94
	Heather	20.42	3.01	88.96	0.62	13.52	1.15
24	Grass	30.36	3.84	84.17	4.1	13.67	1.0
	Heather	30.84	7.77	83.99	8.41	14.26	1.51
30	Grass	23.79	3.74	86.99	1.93	12.43	1.33
	Heather	24.68	7.74	86.47	2.54	13.21	1.73

secretions, may encourage the retention of water droplets on the surface, thus increasing the likelihood of absorption. Comparisons are not available to enable testing of this, although it is only likely to be of any significance in the first few days. After this the dung becomes riddled with tunnels made by beetles (*Aphodius* sp., *Cercyon* sp.) and fly larvae - probably causing a considerable increase in the porosity of the droppings.

Similar variations in moisture content were seen on the grass and heather sites. However, during extraction, on certain days (e.g. day 10) samples from the heather site appeared to have a lower percentage of water, although the difference was not significant. There may be microhabitat differences in the rate of change of moisture content, with dung in the exposed grassland site showing a higher rate of change (Landin, 1961). However, the intervals between collecting days were too great to elucidate any such difference.

Although moisture conditions in the dung varied throughout the 30 day period, the percentage of moisture never fell below 60%. Thus, conditions of high moisture content prevailed, especially important in the early stages of larval development (Gibbons, 1968).

Percentage of Organic Matter

The percentage of ash was determined to give a crude measure of the percentage of dry matter consisting of organic material. This was considered informative in comparative terms as the dung samples aged (Table 3, Fig. 7)

As the animals had been extracted from the subsamples of dung before the percentage of ash was determined, it was expected that the amount of organic matter would decrease per unit weight as it was transformed into the tissues of the feeding animals.

On the heather site, it was found that there was a significant increase ($t = 5.1$, $p < .001$) in the percentage of organic matter between day 1 and day 4. This was followed by a significant decrease ($t = 2.43$, $p < .05$) to day 10, another significant increase to day 16 ($t = 2.28$, $p < .05$)

and a significant decrease to day 30 ($t = 3.0$, $p < .001$).

The reasons for these fluctuations are not clear. They may be due to experimental error, for example, an inadequate dessication procedure. Increases may be partly explained by an increase in the number of bacteria, enchytraeids, nematodes, fungi, protozoa and other organisms left in the subsample after extraction of the macrofauna.

On the grassland site the percentage of organic matter shows an initial significant increase ($t = 7.33$, $p < .001$) from day 1 to day 16 and then a significant decrease ($t = 4.03$, $p < .001$) to day 30. Similarly, the initial increase here may be reflecting an increase in the micro-organisms decomposing the dung.

On both sample sites, the overall decrease in organic matter was only 1 - 1.5%.

Amount of Dry Matter

A decrease in the amount of dry matter with age of dung was expected, due to the feeding, growth and subsequent emigration of fauna and losses caused by leaching and washing away of particles by rain.

The amount of dry matter per sample was determined from the percentage of dry matter and the weight of the sample before faunal extraction (Table 3, Fig. 8).

On the heather site, the dung showed a significant decrease in

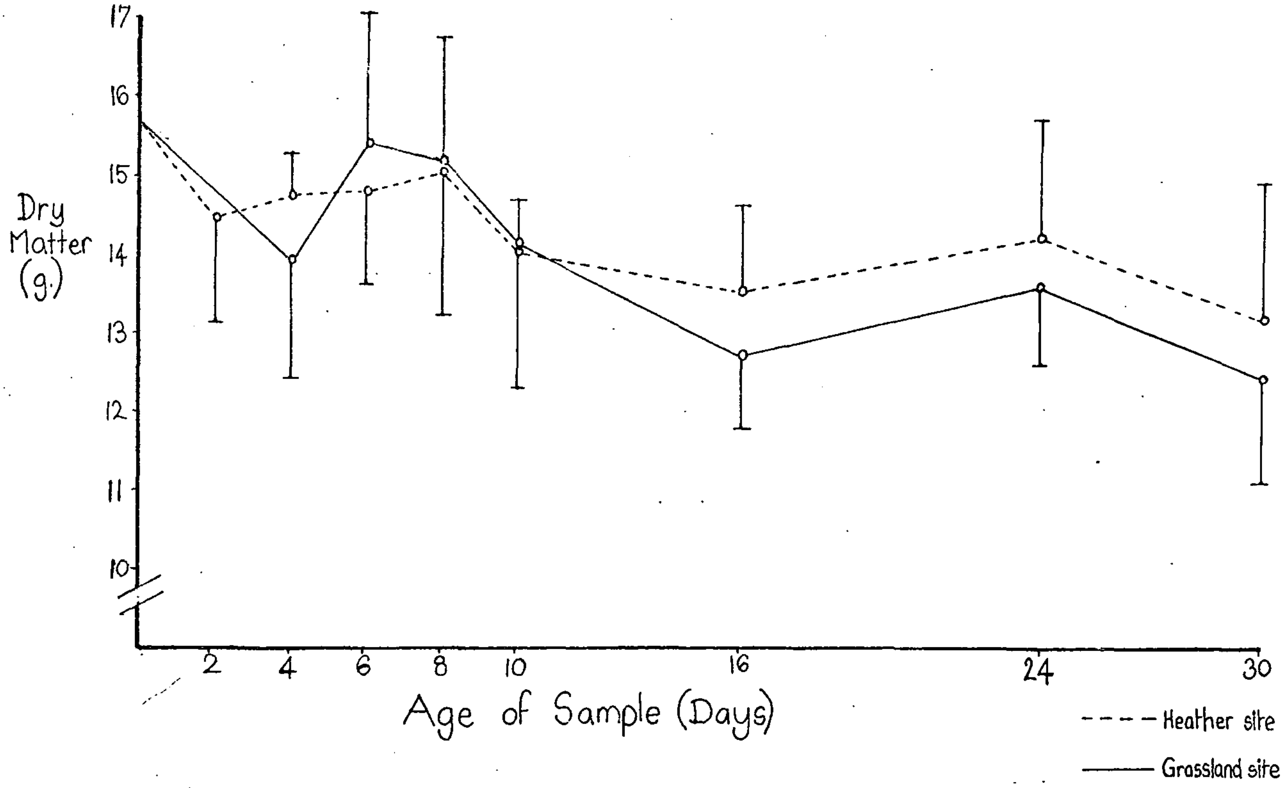


Figure 8 : Amount of Dry Matter with Age of Dung (Standard Errors shown)

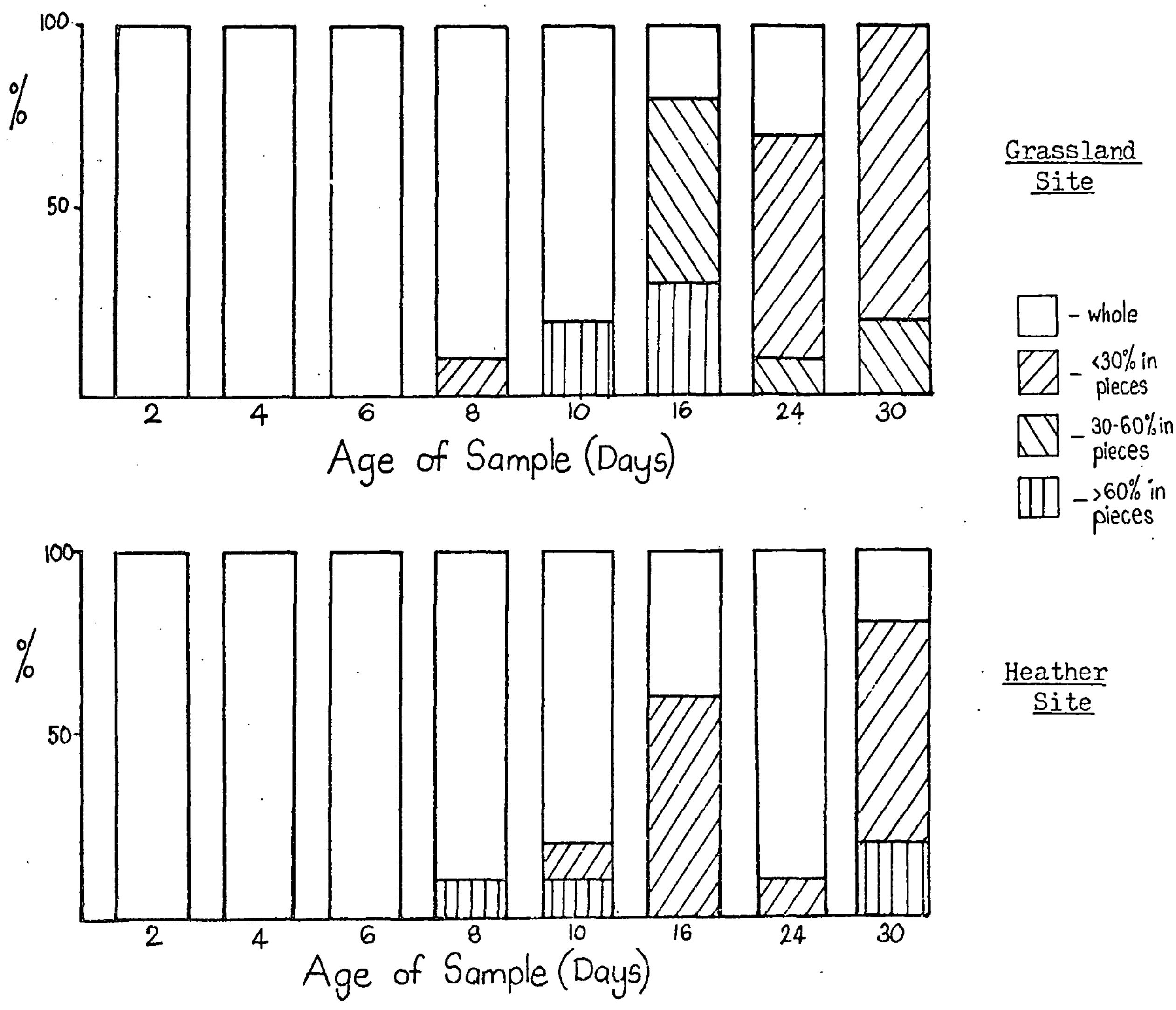


Figure 9 : Disintegration of Dung Samples with Age of Dung

the amount of dry matter ($t = 4.27$, $p < .001$).

On the grassland site, a significant decrease ($t = 3.4$, $p < .01$) was seen initially from day 1 to day 4. This was succeeded by a significant increase on day 6 ($t = 2.2$, $p < .05$) and then a decrease to day 30. The increase may have been due to an increase in the biomass of animals which had migrated in from the outside.

The calculation of the amount of dry matter should ideally be based on the weight of dung with the fauna removed. This was not possible with the extraction procedure used in the present study. A correction factor to eliminate the faunal component was not used as data for the relative biomass of the fauna was not available.

In general terms, it can be seen that there is a decrease in the amount of dry matter per sample with length of exposure. However, given the qualification outlined above, this decrease is probably an underestimate.

Disintegration of Samples

As the dung samples aged and animals burrowed through them, parts began to crumble and fall away. A crude measure was taken of the degree of disintegration and Figure 9 shows the percentage of samples in each category. Dung on both grass and heather sites began to fall apart with age, although samples on the grassland site showed significantly greater disintegration during days 16 to 30 (Mann-Whitney T test, $p < .01$).

Dung that has disintegrated to a certain degree is less suitable for most coprophagous fauna than dung that has retained its integrity. The former is more liable to dessication and allows easier access for predators - both factors are particularly detrimental to coprophagous larvae.

Summary of Changes in Physical Characteristics

The measures used to give an indication of dung decomposition (percentage of dry matter, percentage of organic matter, amount of dry matter, degree of disintegration) gave a varying picture, with changes not always linear with age.

In overall terms, the 30 day dung samples showed less dry matter, less organic matter and more disintegration than at the beginning of the period. The changes were essentially the same on both heather and grassland sites, although on the grassland site the dung samples showed more rapid disintegration.

The percentage of water varied continuously, apparently in response to rainfall, but did not fall below 60%. Thus, dessication was not likely to have been a problem to thin-cuticled dung-inhabiting fauna, although water-logging conditions might have been.

II. DUNG-INHABITING FAUNA

During the 30 day period, 6,258 individuals and 2,372 eggs were collected from the dung samples. The fauna comprised representatives

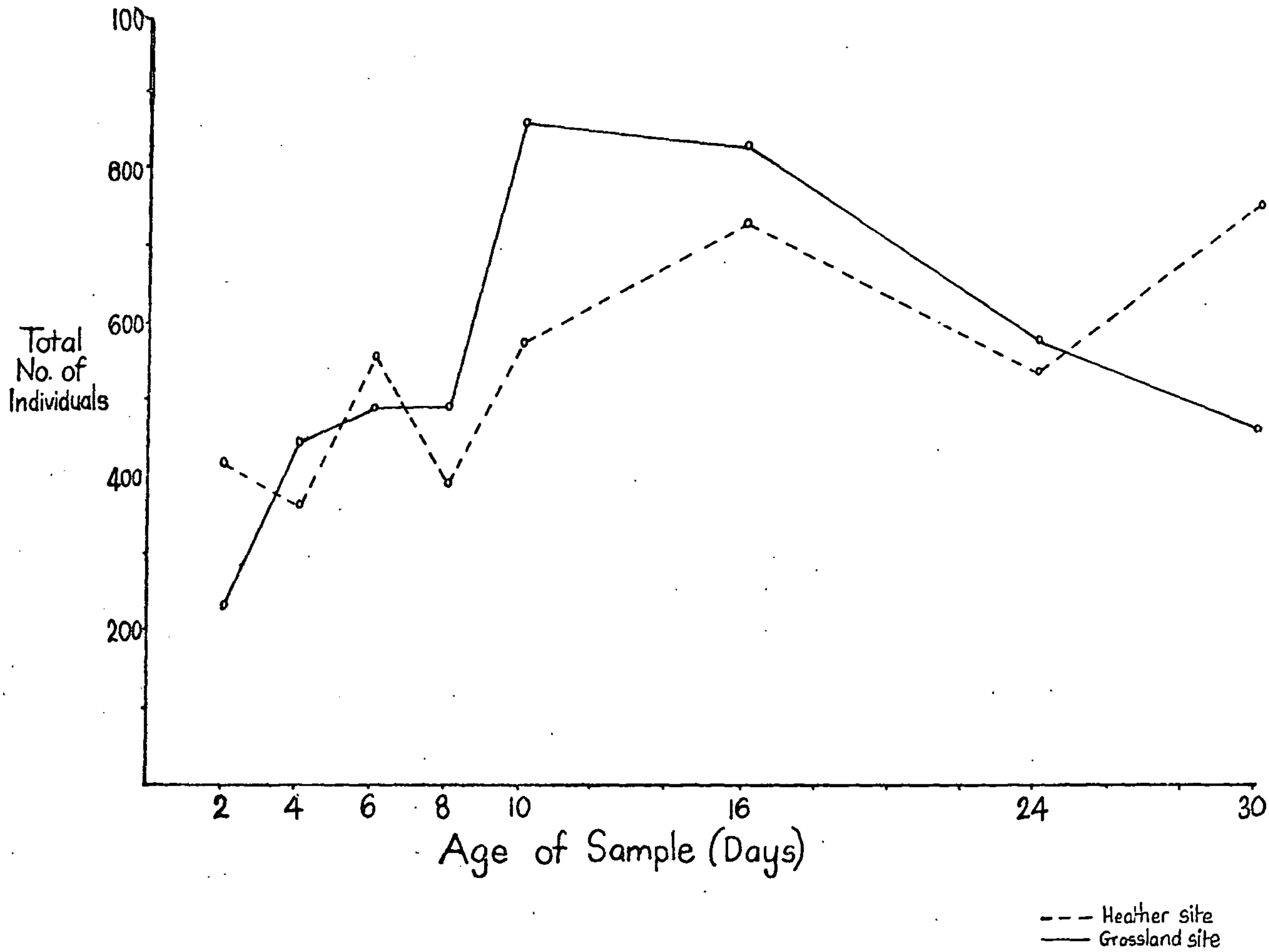


Figure 10 : Total Number of Individuals with Age of Dung

from five different groups: Diptera, Coleoptera, Acarina, Annelida, Gastropoda. More detailed information of the families and in some cases genera and species found on each sampling day and each site is given in Appendix 1. Illustrations of a selection of the fauna are presented in Appendix 2.

Changes in Numbers with Age of Dung and Microhabitat

The total numbers of individuals in the samples were found to increase to a maximum at 10 days on the grassland site and 16 days on the heather site (Fig. 10).

To obtain more detailed information on the changes in the invertebrates comprising these totals, the fauna was categorised as follows:

(1) Dipteran Eggs - generally whitish and elongated in shape.

(2) Beetle Eggs - whitish, more spherical with no exterior markings.

(3) Dipteran Larvae - includes Cyclorrhaphous larvae and Nematoceran larvae.

(4) Other Beetle Larvae - comprising Staphylinidae larvae, active campodeiform larvae with four-segmented legs, and Hydrophilidae larvae, grub-like with atrophied legs and a well-developed head. Far less frequent but also included in this category are Carabid beetle larvae, campodeiform larvae with five-segmented legs, and Elaterid larvae, elongated, sluggish in movement and tough-skinned.

(5) Staphylinidae adults.

(6) Hydrophilidae adults.

Table 4 : Mean Numbers (and Standard Deviations) of Faunal groups with Age and Site of Dung

AGE OF DUNG

		2		4		6		8		10		16		24		30	
		$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ
Dipteran Eggs	Grass	13.1	16.0	11.3	14.7	11.4	14.8	0.3	1.0	4.5	6.6	0.8	1.8	0.3	0.7	0	0
	Heather	21.3	22.12	17.7	13.7	11.4	14.8	20.0	18.3	10.3	9.2	3.1	2.6	0.2	0.6	0	0
Beetle Eggs	Grass	0	0	1.5	1.8	2.2	3.8	10.9	12.4	19.9	15.1	32.8	29.0	11.0	10.6	2.38	3.93
	Heather	0	0	1.3	2.9	2.4	3.9	4.6	5.6	8.5	10.1	8.8	8.9	3.0	4.5	2.7	6.2
Dipteran larvae	Grass	3.0	9.1	15.0	15.4	10.4	9.1	10.3	8.6	25.7	17.7	18.4	15.7	6.0	6.4	4.8	2.6
	Heather	16.9	21.8	13.8	9.1	34.6	30.3	2.7	3.2	23.7	15.3	55.8	19.4	48.6	38.1	31.2	38.2
Beetle larvae (not Aphodius)	Grass	0	0	0	0	0	0	2.3	4.2	7.2	3.5	15.4	9.5	11.9	6.5	4.5	2.4
	Heather	0	0	0.1	0.3	0	0	0.5	1.3	1.6	2.0	1.4	1.9	1.0	1.2	4.0	3.4
Staphylinid adults	Grass	2.1	2.1	3.2	2.8	5.8	4.1	6.5	3.9	10.9	7.8	3.6	3.4	0	0	0	0
	Heather	0.4	1.0	0.4	0.8	2.0	2.4	1.3	1.2	3.4	4.0	0.2	0.4	0.8	0.8	0.3	0.7
Hydrophilid adults	Grass	0.9	1.1	3.9	3.1	6.8	3.9	3.4	3.3	6.7	4.5	2.5	2.1	0.5	1.3	0	0
	Heather	0.1	0.3	0.2	0.4	0.5	0.5	1.0	1.3	3.0	4.1	1.8	1.8	0.2	0.4	0.7	1.1
Aphodius adults	Grass	4.6	3.0	5.8	2.3	6.6	3.3	5.5	2.2	2.0	1.6	0.5	0.9	0.3	0.7	0	0
	Heather	2.1	3.4	2.3	2.0	2.6	2.0	6.2	5.0	3.4	2.3	0.5	0.9	0	0	0	0
Aphodius larvae	Grass	0	0	0	0	0	0	0	0	0	0	3.0	3.46	25.3	11.9	30.6	6.2
	Heather	0	0	0	0	0	0	0	0	0	0	0.1	0.3	4.0	8.6	33.4	23.3
Mites	Grass	0	0	4.2	2.7	4.8	4.0	9.0	3.2	9.2	6.2	5.2	2.7	2.2	2.9	4.1	3.9
	Heather	0.3	1.0	0.6	0.8	1.8	1.3	2.9	2.0	2.8	3.2	1.7	1.8	1.2	1.7	3.5	3.3

(7) Aphodius adults.

(8) Aphodius larvae - typical scarabaeiform larvae: 'C'-shaped with a well-developed head, short thoracic legs and a soft, fleshy body.

(9) Acarina.

(10) Others - Annelida, Gastropoda, Ptiliidae etc.

The changes in the numbers of individuals comprising these groups, with the age of the dung and between grass and heather microhabitats are presented in Table 4 and Figures 11-20, and are considered in detail below.

Analyses of variance (simple randomized design) showed that for each of the groups analysed (groups (1)-(9)), the age of the dung was a significant variable in determining numbers. The 'F' values of these analyses are shown in Table 5.

Table 5 : 'F' Values obtained from the Analyses of Variance (with significance levels

		Faunal Group								
		Fly Eggs	Beetle Eggs	Fly larvae	Beetle larvae	Staphylinidae	Hydrophilidae	Aphodius adults	Aphodius larvae	Mites
Site	Grass	3.4, $p<.01$	7.3, $p<.001$	4.1, $p<.01$	16.1, $p<.001$	7.8, $p<.001$	8.3, $p<.001$	16.7, $p<.001$	63.4, $p<.001$	7.5, $p<.001$
	Heather	4.6, $p<.001$	2.4, $p<.05$	5.0, $p<.001$	6.4, $p<.001$	3.8, $p<.01$	4.5, $p<.001$	7.1, $p<.001$	20.8, $p<.001$	3.0, $p<.01$

(1) Dipteran Eggs (Fig. 11)

Most dipteran eggs were found on the first day of sampling: after two days of exposure. The numbers then decrease and few are found on or after day 16. There appear to be more dipteran eggs on the heather than

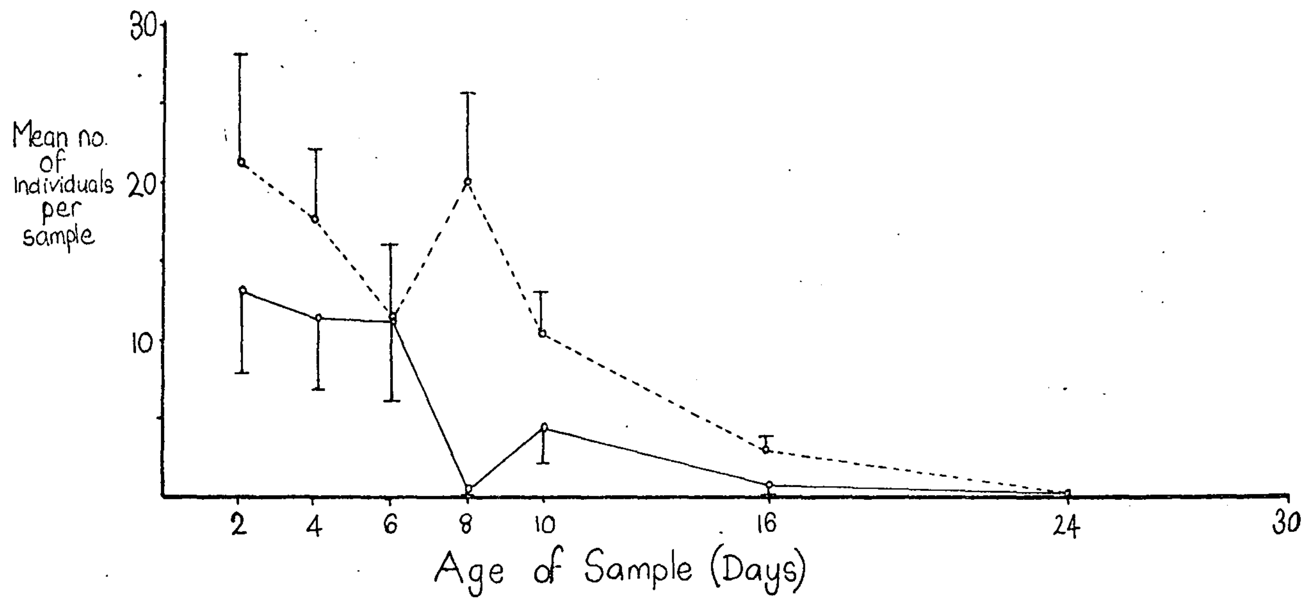
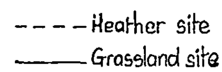


Figure 11 : Mean Number of Dipteran Eggs with Age of Dung (standard errors shown)



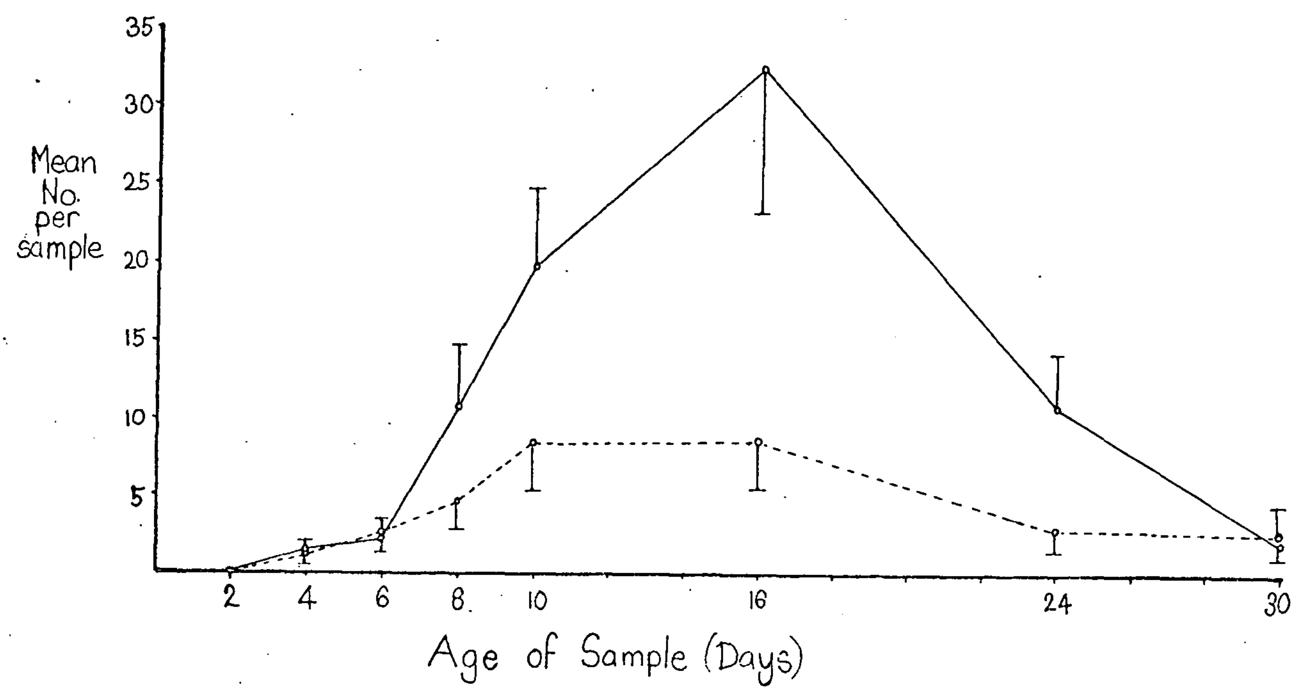


Figure 12 : Mean Number of Beetle Eggs with Age of Dung (Standard Errors shown)

on the grassland site and in five out of the six sampling days on which more than 5 eggs were found in the ten samples, the number was higher on the heather site. The decrease in numbers with age appears to be more rapid on the grassland site than on the heather site, with a significant decrease ($t=2.53$, $p<.05$) being found on day 8 on the grassland but not until day 16 on the heather site ($t = 2.59$, $p<.05$).

The problem with a measure of the number of dipteran eggs is that as a measure of the suitability of the habitat for dipteran reproduction, it gives no indication of the number of females that have visited the dung, as the size of the brood varies from a few hundred to only a few eggs. A more valid measure would have been the proportion of samples on a particular day containing dipteran eggs. However, with the relatively small sample size used in this study, it was felt that an indication of the number of eggs provided more information.

(2) Beetle Eggs (Fig. 12)

The qualification of using the numbers of eggs as a measure of habitat suitability described above, also applies to this category but to a lesser extent because the brood size of Coleoptera is generally smaller than that of Diptera. Each egg hatches into a single individual although the papery case deposited by the Hydrophilidae constitutes a single brood and hatches into 3-8 larvae.

Few beetle eggs were found in the period up to 6 days and then numbers increased to a maximum at 16 days. This was followed by a decrease in numbers with few found in dung exposed for 30 days. It can be seen from Figure 12. that on days 8 - 24, when most of the beetle eggs are found, more are found on the grassland site than on the heather site (day 16, day 24; $t = 2.5$, 2.19 respectively, $p < .05$).

(3) Dipteran Larvae (Fig. 13)

This group comprise mainly Scatophaga, Borboridae and Anthomyidae larvae with Nematocera larvae found in the later stages of dung ageing.

The numbers of dipteran larvae on the grassland site showed an increase to a maximum on day 10 and a subsequent decrease.

Great fluctuations were seen on the heather site with an initial significant increase ($t = 2.08$, $p < .1$) to day 6 followed by a significant decrease on day 8 ($t = 3.31$, $p < .01$). The numbers of larvae then increased significantly again showing a maximum on day 16 ($t = 8.54$, $p < .001$). Numbers were lower on day 30 although the dung still contained a mean of 31 individuals per sample. The peak in numbers on day 6 followed by the trough on day 8 can be explained in various ways. The initial peak may have comprised a single generation of larvae which might have hatched or migrated in a pre-pupal stage by day 8. Identification of the larvae in their various developmental stages was not sufficient to determine the validity of this explanation. Alternatively, fewer eggs may have been laid on the particular dung samples collected on day 8 as, being towards the middle of the two heather paths, approaching flies would be more likely to oviposit on outer dung samples.

On day 6 and on days 16 to 30, significantly greater numbers of larvae were found on the heather site than on the grassland site ($t = 3.99$, $p < .05$).

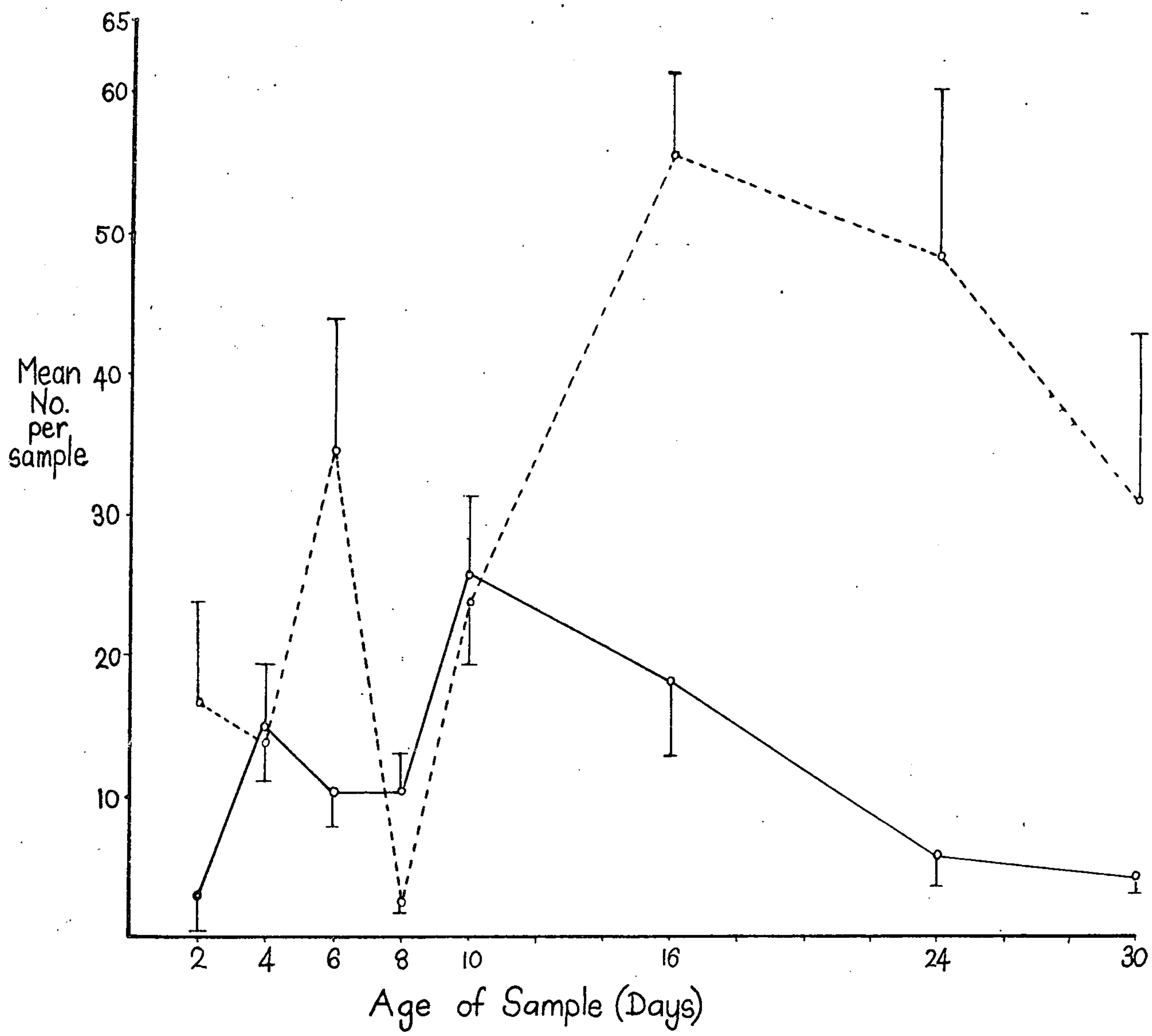


Figure 13 : Mean Number of Dipteran Larvae with Age of Dung (Standard Errors shown)

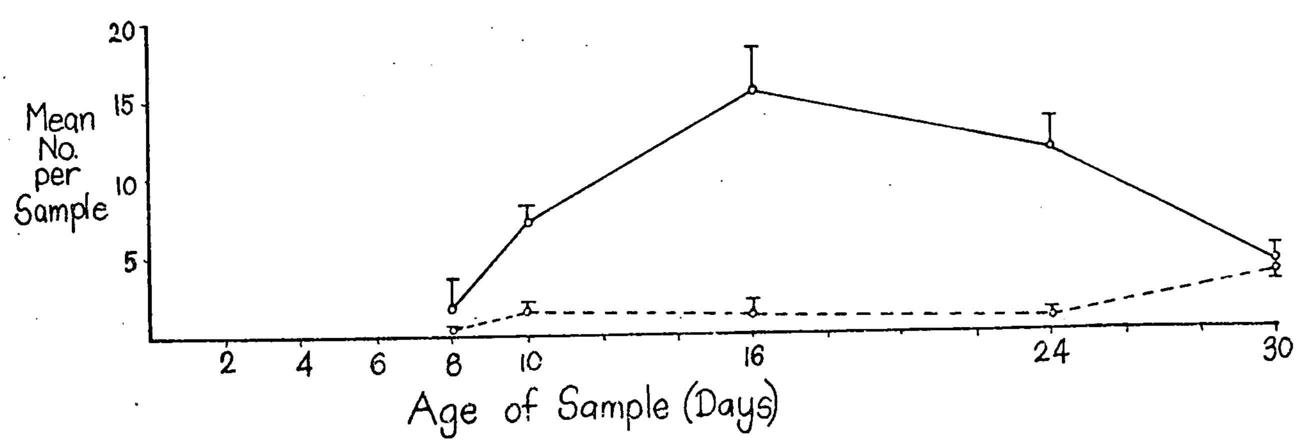


Figure 14 : Mean Number of Beetle Larvae (not Aphodius) with Age of Dung (Standard Errors shown)

Cyclorrhaphous pupae were found on days 24 and 30 with higher numbers on the heather site. Most of these, when hatched, were found to be Scatophaga spp. which are known to pupate both in dung and in soil (Gibbons, 1968). For this reason, the pupae were not included in the quantitative analyses.

If the nematoceran larvae are considered separately, it is found that they occured after day 10 on both grass and heather sites but in low numbers compared with the cyclorrhaphous larvae. These larvae comprise the families; Psychodidae, Mycetophilidae, Cecidiomyiidae and Chironomidae. These are general saprophages and are commonly found as dung ages.

As in the case of dipteran eggs, a measure of the number of larvae in the samples does not give an indication of the number of adult flies that have visited the samples. However, the number of larvae gives an indication of the suitability of the dung for dipteran survival. Another point to be made here is that a measure of the numbers of individuals gives no indication of changes in biomass. Thus, although a decrease in numbers of larvae is found on day 30, many of the individuals concerned are third instar larvae or in the pre-pupal stage, therefore their total biomass is probably greater than that of the more numerous but smaller larvae found earlier in the sampling period.

(4) Other Beetle Larvae (Fig. 14)

Beetle larvae (excluding Aphodius larvae) were first seen on day 8 with numbers increasing to day 16 on the grassland site then decreasing. There were very few beetle larvae on the heather site at all times and on days 10, 16 and 24, significantly greater numbers of larvae were found on the grassland site ($t = 4.41, 4.58, 5.19$, $p < .001$). The larvae comprise mostly hydrophilid and staphylinid larvae in approximately equal numbers. Small numbers of carabid and elaterid larvae were found.

(5) <u>Staphylinid Adults (Fig. 15)</u>

Staphylinid adults were found after 2 days and their numbers increased significantly ($t = 3.42$, $p < .01$) to a maximum at 10 days followed by a significant decrease ($t = 2.5$, $p < .05$). On the grassland site, no individuals were found on days 24 and 30. On the heather site, staphylinid adults were found on these days albeit in very low numbers.

Significantly more staphylinid adults were found on the grassland site than on the heather site (Wilcoxon matched pairs test, $p < .05$).

(6) <u>Hydrophilid Adults (Fig. 16)</u>

Hydrophilid adults are found to increase during days 2 to 10 with numbers falling gradually and few found on days 24 and 30. On the grassland site, a decrease is found on day 8 followed by an increase on day 10. The decrease approaches significance ($t = 2.093$, tabled value for the 5% level of significance is 2.101), but the reason for this decrease is not clear.

Numbers of individuals are significantly higher on the grassland site than on the heather site (Wilcoxon matched pairs test, $p < .05$)

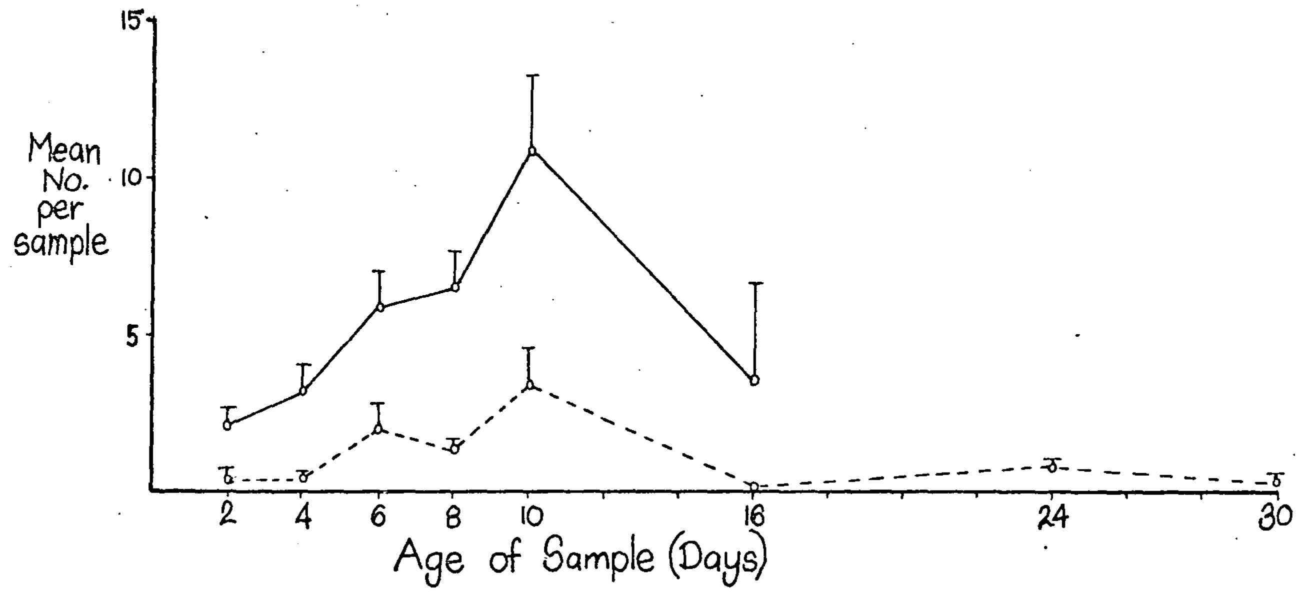


Figure 15 : Mean Number of Staphylinid Adults with Age of Dung (Standard Errors Shown)

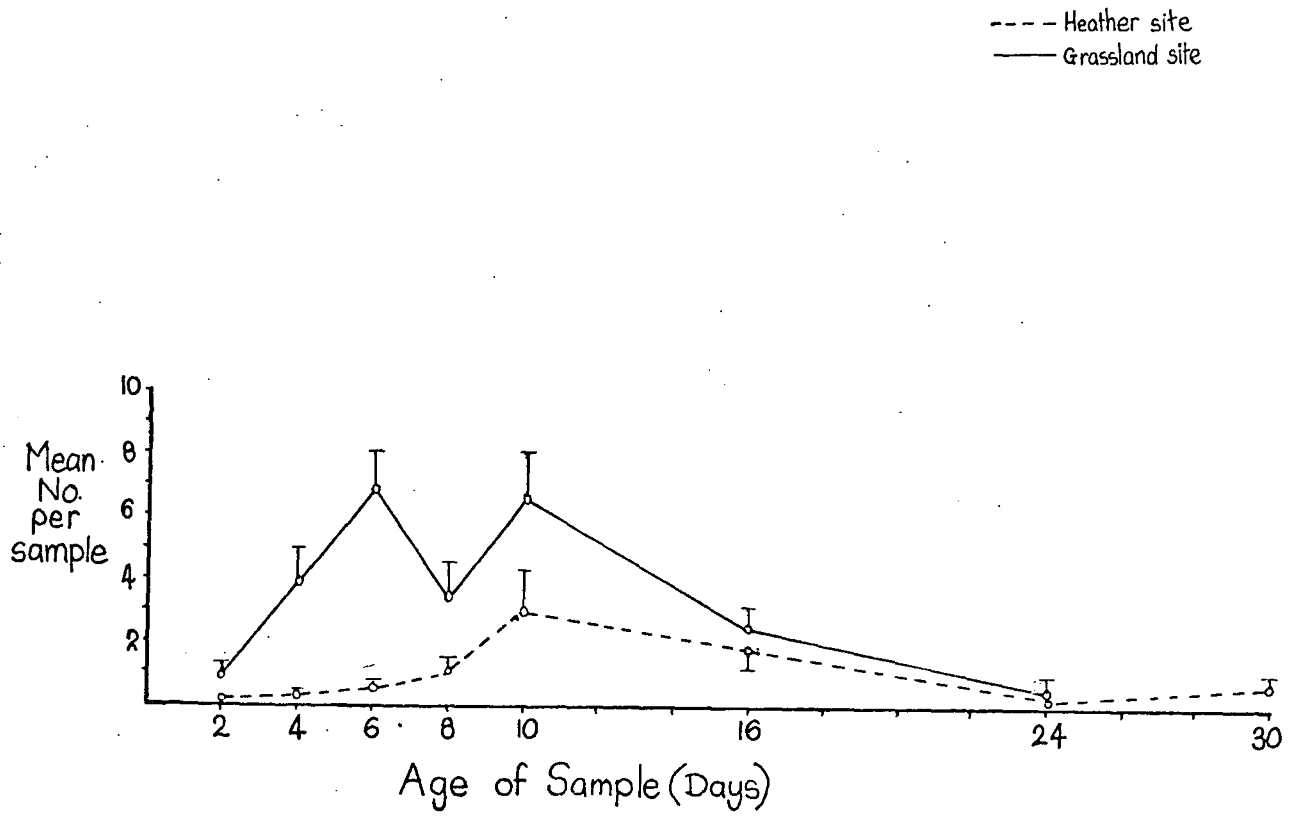


Figure 16 : Mean Number of Hydrophilid Adults with Age of Dung (Standard Errors shown)

(7) Aphodius Adults (fig. 17)

Aphodius adults are found after 2 days and increase to a maximum at 6-8 days. Few are found after 10 days. In the 2 to 6 day period, significantly more Aphodius adults are found on the grassland site than on the heather site ($t = 10.16$, $p < .001$).

Most of the Aphodius adults comprised two species ; A. ater (Deg.) and A. lapponum (Gyll.). From Figure 18 which shows the total numbers of each of these species, it can be seen that A. lapponum is found from 2 days onwards whereas A. ater is found after 4 days and particularly on the grassland site, their numbers remain higher for longer than those of A. lapponum.

(8) Aphodius Larvae (Fig. 19)

Aphodius larvae are not found until day 16 and then numbers show an increase to the last sampling date on day 30. On day 24, there are significantly more larvae on the grassland site than on the heather site ($t = 4.95$, $p < .001$), but on day 30, both sites have similar numbers of larvae. This may be the result of a developmental lag on the heather site. Support for this comes from the fact that on day 30, third instar larvae comprise 20.8 % of the larval population on the grassland site but only 3.9 % on the heather site. Aphodius eggs may have been deposited later on the heather site and indeed the maximum numbers of Aphodius adults on the heather site is later than on the grassland site.

A few Aphodius larvae were found in the soil cores under the dung particularly on day 16 on the grassland site. It had rained for 4 days

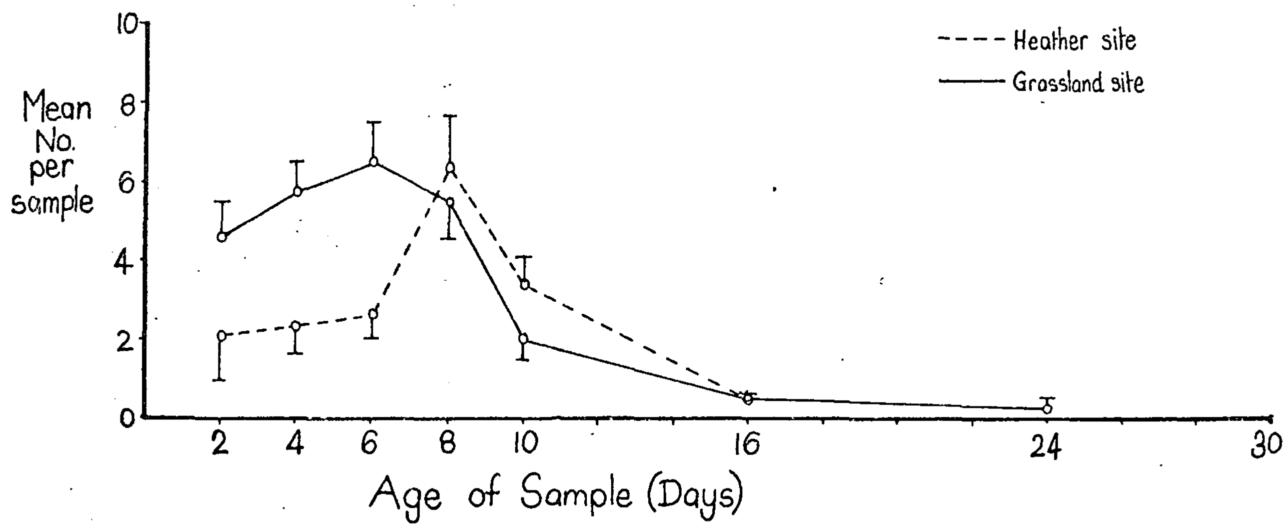


Figure 17 : Mean Number of Aphodius adults with Age of Dung (Standard Errors shown)

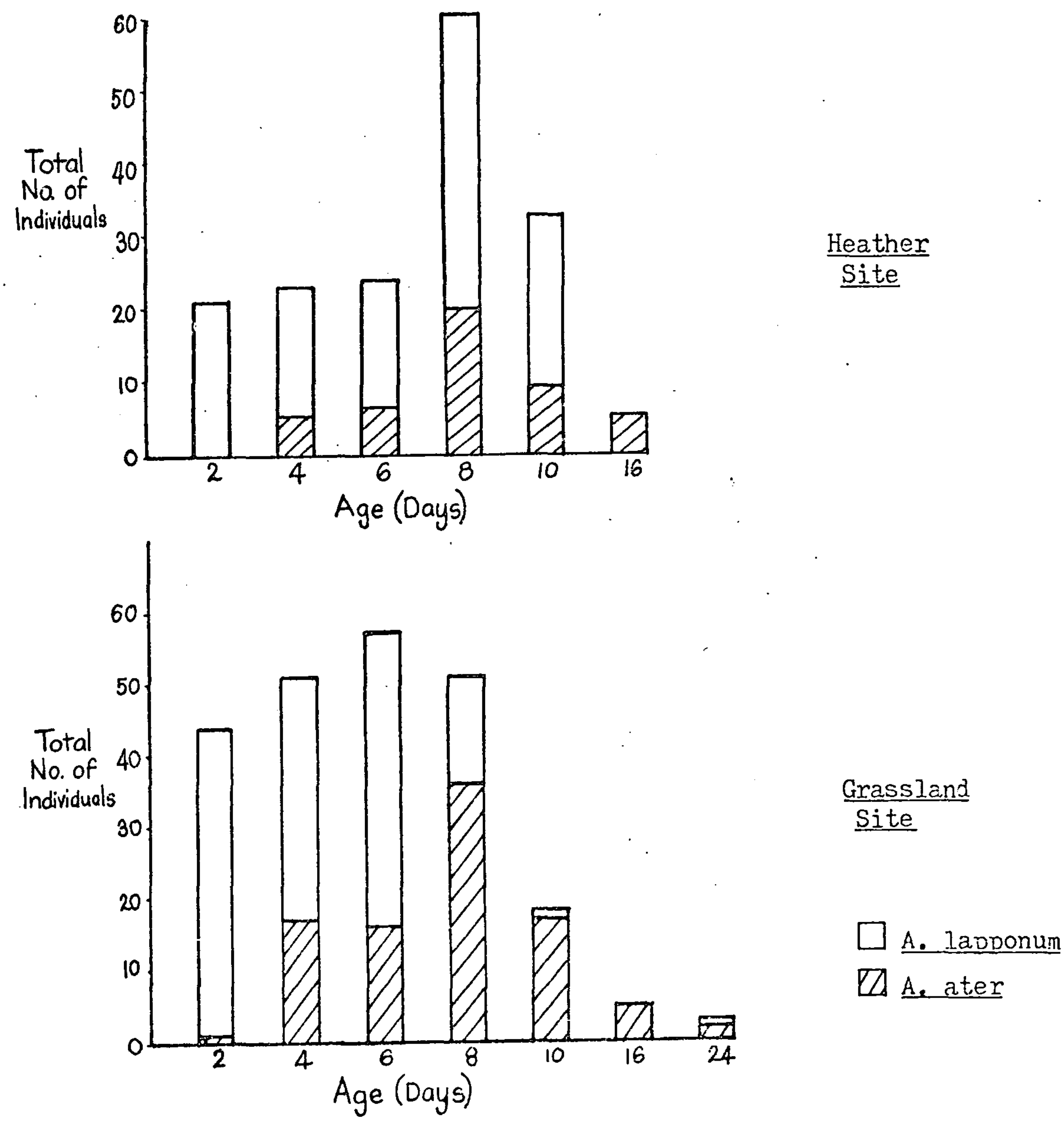


Figure 18 : Total Numbers of A. lapponum and A. ater with Age of Dung

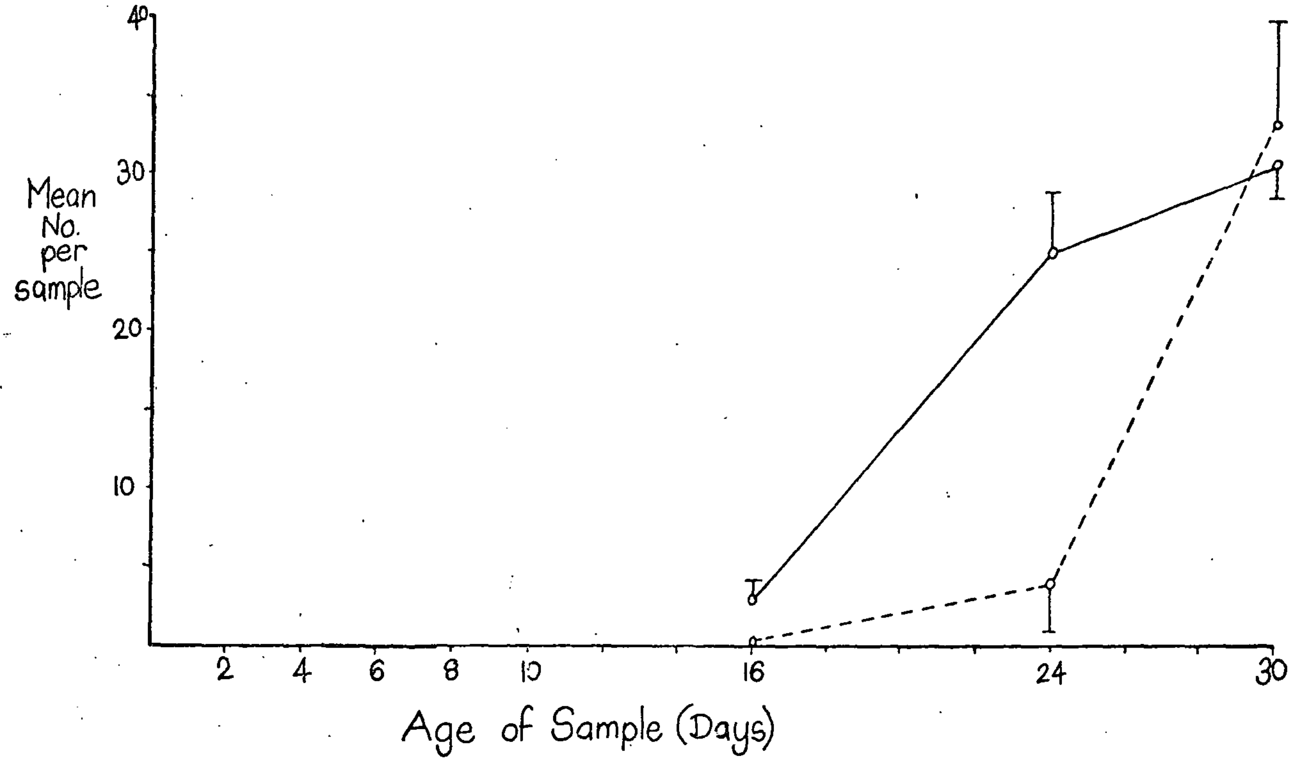


Figure 19 : Mean Numbers of Aphodius larvae with Age of Dung (Standard Errors Shown)

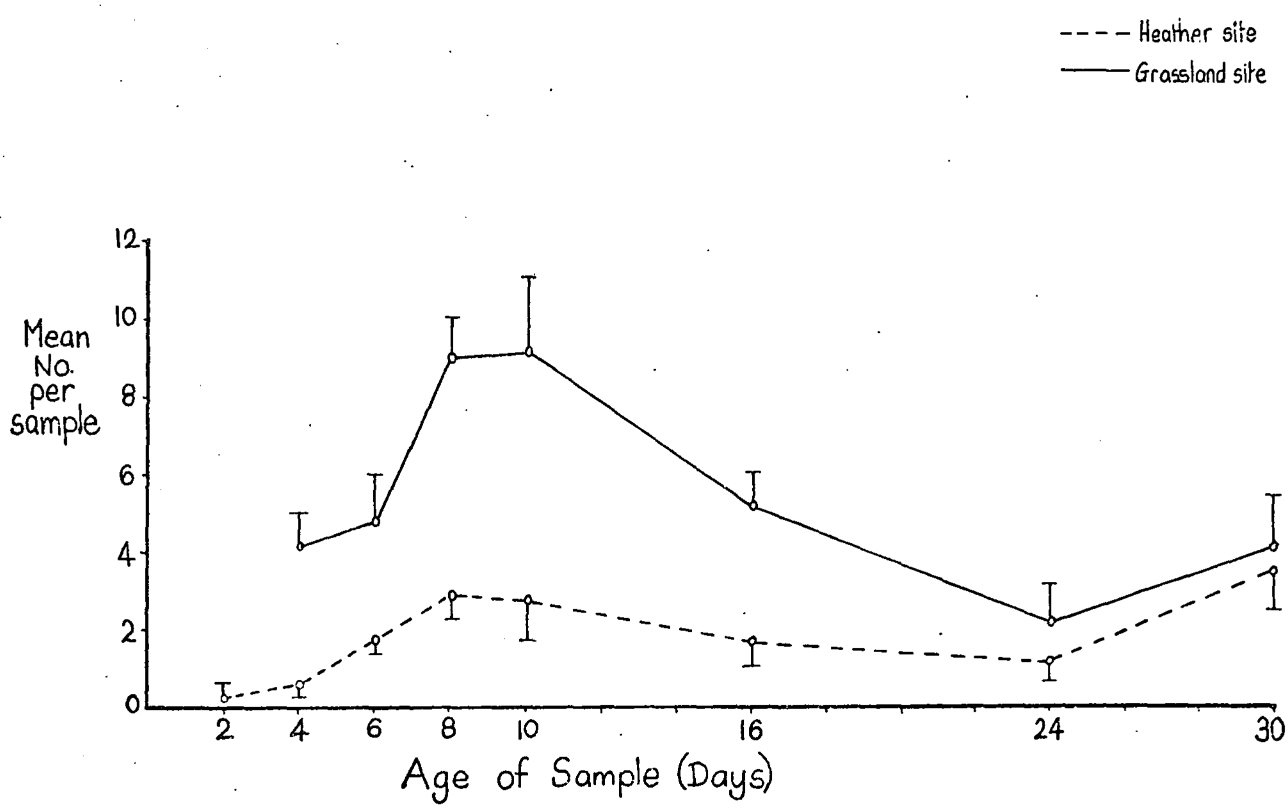


Figure 20 : Mean Number of Mites with Age of Dung (Standard Errors Shown)

previously and thus to avoid waterlogging conditions, some of the larvae may have migrated from the dung.

(9) Mites (Fig. 20)

It can be seen from Figure 20 that there are significantly greater numbers of mites on the grassland site than on the heather site (Wilcoxon matched pairs test, $p < .05$). Mites are found in low numbers initially and then increase to a maximum at 8-10 days followed by a decrease to day 24. On day 30, numbers increase on both sites, which, although not statistically significant, shows that the trend of a decrease in numbers has been halted. This may be due to the arrival of different species, in particular mites forming part of the general soil fauna. Due to difficulty in identifying mites and the scarcity of information on the feeding biology of different species, this hypothesis could not be tested.

(10) Other Groups of Fauna

Other animals were found in low numbers and therefore not included in the quantitative analyses. Tipulidae larvae were found, presumably using the dung as shelter and two Lepidoptera larvae were found in beetle tunnels in their pre-pupal stages. Worms (Bimastos eiseni Levinsen.) were found in low numbers after day 16 with the highest proportion on the grassland site. Some slugs were found on the surface of dung samples and occasional Ptiliidae beetles were found in the latter stages of dung ageing.

Summary of Changes in Numbers within Faunal Groups

Figure 21 gives a summary of changes in abundance within groups as the dung ages. The scales for each group are different, therefore numbers are relative within groups but not between groups.

Grassland Site

The first animals to appear on the dung samples are flies, as shown by the eggs deposited there, Aphodius adults and some staphylinid and hydrophilid adults.

Over the next eight days, increasing numbers of staphylinid and hydrophilid adult beetles colonise the dung. Dipteran larvae are found in increasing numbers as are mites. Aphodius adults also show an increase in numbers during this period but this is followed immediately by a relatively rapid decrease.

In the following period (10-16 days), all these groups show a decrease in numbers (i.e. Staphylinidae and Hydrophilidae adults, dipteran larvae and mites). Beetle eggs and staphylinid and hydrophilid larvae are found in increasing numbers.

Between 16 and 30 days of dung ageing, fewer numbers of staphylinid, hydrophilid larvae and beetle eggs are found. Aphodius larvae however, show a continued increase after 16 days and although there may be a further increase after the end of the sampling period of 30 days, it is unlikely to be large, as few beetle eggs were found on day 30. Thus, the Aphodius larval population is probably at its maximum

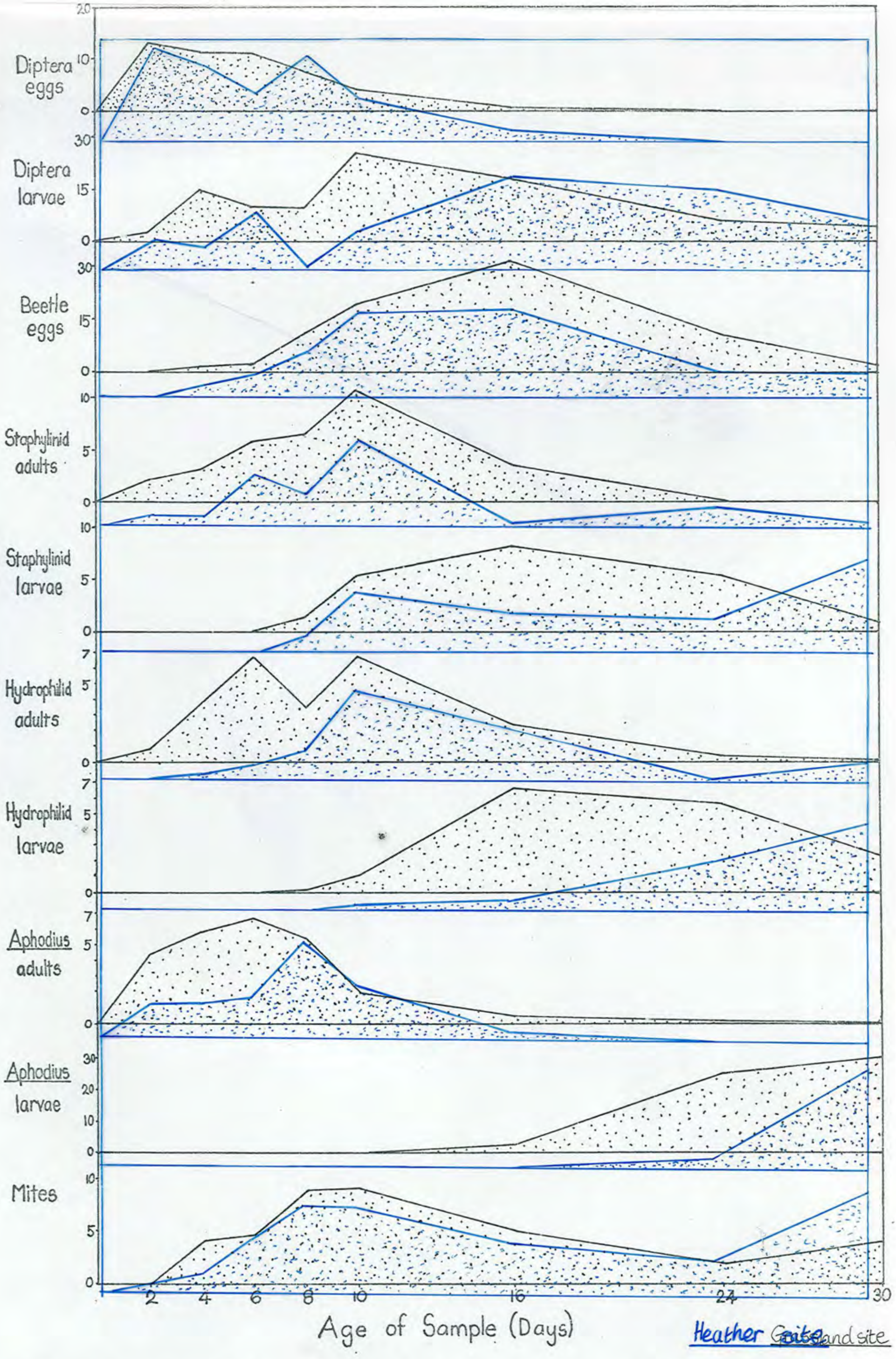


Figure 21 : Mean Numbers of Individuals in each Group with Age of Dung

around 30 days. The number of mites remains fairly steady in the 16-30 day period and there is an indication of a possible increase after 30 days.

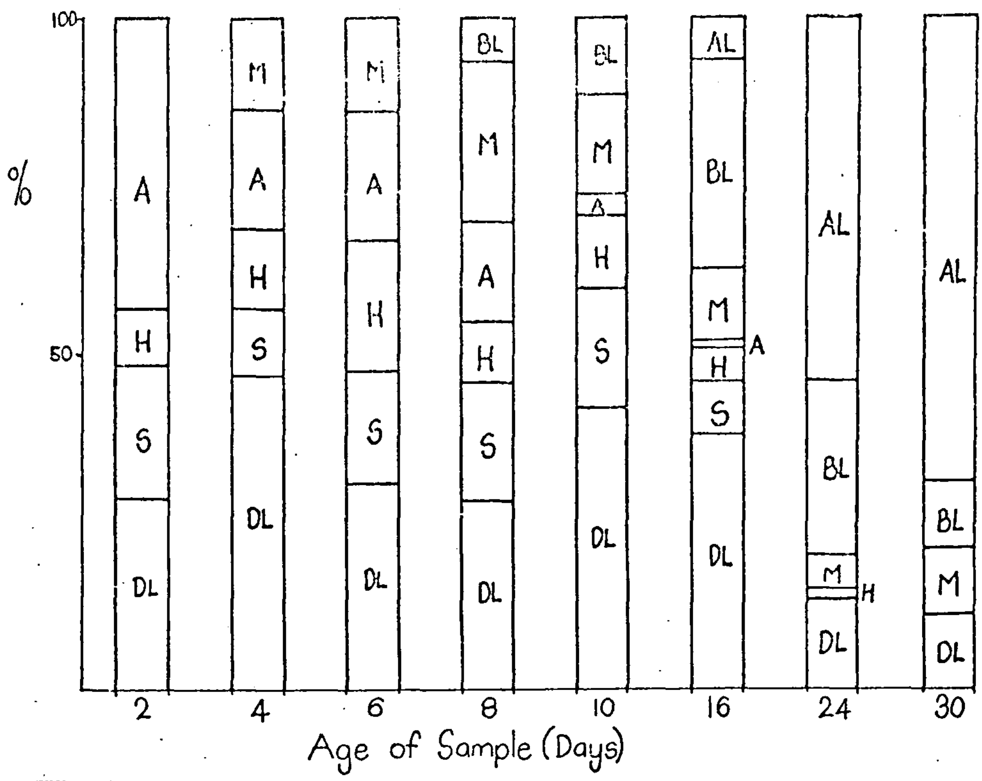
Heather Site

A similar picture of 'succession' of the various groups is seen on the heather site, although in some cases the changes are seen at a later stage of dung ageing. Thus, hydrophilid and *Aphodius* adults have their abundance peaks two days later than on the grassland site and staphylinid and hydrophilid larvae as well as *Aphodius* larvae show a more gradual increase on the heather site and no sign of a decrease during the sampling period.

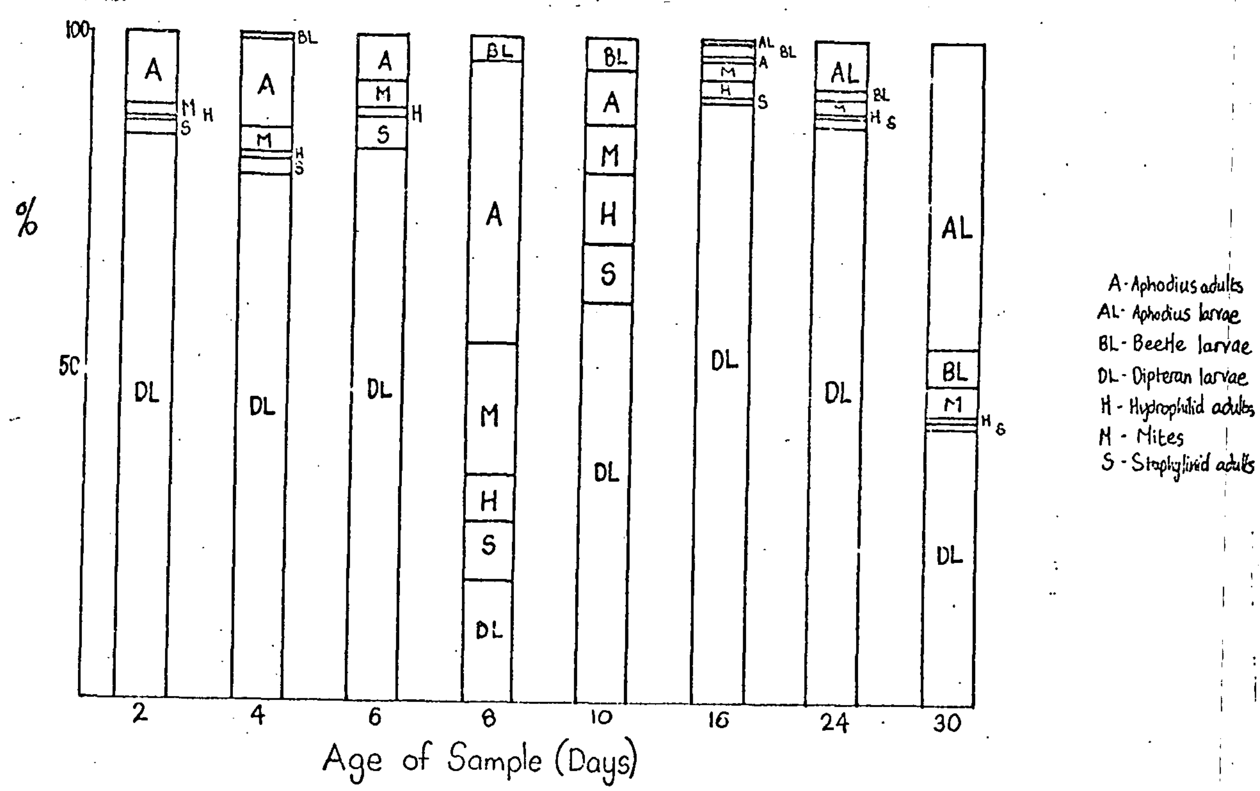
Relative Abundance of Faunal Groups

The numbers of individuals in each group was calculated as a percentage of the total number of individuals for each day on the the grass and heather sites separately. The results are shown in Figure 22 and Table 6 gives the group totals. Fly and beetle eggs were not included in this analysis as a description of the relative numbers of only those groups exerting a direct influence on the micro-habitat was considered to be more informative.

It can be seen from Figure 22, that on the grassland site, *Aphodius* adults form the most numerous group on day 2 and dipteran larvae on day 4. On days 4-16, the numbers of individuals are fairly evenly distributed among the groups, with dipteran larvae in relatively



Grassland Site



Heather Site

Figure 22 : Relative Abundance of Faunal Groups with Age of Dung

Table 6: Total Number of Individuals of each Group found on each Day and on each Site

Day	Site	Dipteran Larvae	Aphodius Larvae	Other Beetle Larvae	Staphylinidae	Hydrophilidae	Mites	Aphodius Adults	Totals
2	Grass	30	0	0	21	9	0	46	106
	Heather	169	0	0	4	1	3	21	198
4	Grass	150	0	0	32	39	42	58	321
	Heather	138	0	1	4	2	6	23	174
6	Grass	104	0	0	58	68	48	66	344
	Heather	346	0	0	20	5	18	26	415
8	Grass	103	0	23	65	34	90	55	370
	Heather	27	0	5	13	10	29	62	146
10	Grass	257	0	72	109	67	92	20	617
	Heather	237	0	16	34	40	28	34	389
16	Grass	184	30	154	36	25	52	5	486
	Heather	558	1	14	2	18	17	4	614
24	Grass	60	253	119	0	5	22	3	462
	Heather	484	40	10	8	2	12	0	556
30	Grass	38	245	36	0	0	33	0	352
	Heather	312	334	40	3	7	35	0	731

high proportions throughout this period. On days 24 and 30, Aphodius larvae comprise the greatest proportion of individuals.

On the heather site, a different situation is evident. On most days, dipteran larvae comprise over 60 % of the total fauna, with individuals of other groups present but in relatively low numbers. Day 8 is unusual in that it shows relatively lower numbers of dipteran larvae corresponding with higher numbers of Aphodius adults. Possible explanations for this decrease in dipteran larvae were outlined in Section (3). On day 30, Aphodius larvae and dipteran larvae in approximately equal proportions comprise over 80 % of the total fauna under investigation.

Thus, it would appear that on the grassland site, no single group is dominant in terms of numbers, whereas on the heather site, dipteran larvae are dominant on most days.

As individuals from each group and within groups differ in size and in biomass, a more informative measure of their relative importance would have included biomass as well as numbers of individuals. Unfortunately, the numbers of animals obtained did not permit calculation of biomass.

Analysis of Diversity

To obtain more detailed information on temporal changes in species composition and their relative abundance, an index of diversity was used which enabled calculation of the amount of community change, i.e. the rate of succession.

This analysis was only carried out on the coprophages on the two sampling sites and the species assigned to this trophic level are marked with a 'C' in Appendix 1. Similar analyses were not carried out on the remaining species as these formed a heterogenous group of obligate and facultative carnivores and some species of uncertain trophic status.

The species composition used in the analysis is an estimate for the reasons outlined below.

(i) Borborid larvae: the relative numbers of the different species of Borboridae could not be determined from the larval forms. From cultured larvae, Borborus sp. was found to be the most numerous therefore this larval category was designated as a single species.

(ii) Other Cyclorrhaphous larvae: similarly, identification of the larval groups was not possible but from larvae reared to adults, three species were found in equal proportions; Scatophaga stercoraria, Scatophaga furcata, Chlorotica sp.. Therefore, the larvae were assigned to three species in equal numbers.

(iii) Aphodius larvae were counted as a single species, as identification of the first and second instar larvae was not possible. Extrapolation from proportions of the third instar larvae would have been erroneous due to possible different rates of development of the component species.

(iv) Staphylinidae larvae and adults were considered as different species.

(v) Mites were categorised superficially but not identified. The more active mites and those apparently associated with Aphodius beetles were considered as predatory and not included in the analysis. The remaining mites represented 40 % of the total mites found and this figure is more likely to be an underestimate than an overestimate of coprophagous species, as predatory species are generally found in relatively lower numbers.

The inclusion of the 'species' described above in the analysis of diversity was considered to provide more valid information than their total exclusion, in spite of the fact that this was probably an underestimate of the species number. If only a single individual of a species was found through the sampling period, its prescence was not considered in the analysis.

Number of Species

Figure 23 and Tables 7 and 8 show the number of species found throughout the sampling period on each site. 34 coprophagous species were found on the grassland site with the larval forms of two staphylinid species, bringing the total to 36 species (2305individuals). The number of species shows a rapid increase to day 4 and remains fairly steady on days 8 to 16 and then falls again on days 24 and 30.

On the heather site, fewer species were found (24 species and 2972 individuals). The number of species shows an initial increase to day 6 followed by a decrease on day 8. A gradual increase is then apparent to day 24.

Diversity

To obtain a measure including both the number of species and the evenness of distribution of individuals among the species, the Shannon-Wiener index of diversity (H') was calculated for each day using the following formula:

$$H' = -\Sigma \left[\left(\frac{n_i}{N}\right) \log_e \left(\frac{n_i}{N}\right) \right]$$

where n_i is the number of individuals in species i.

N is the total number of individuals.

The results are shown in Figure 24 and Tables 8 and 7.

On the grassland site, the greatest diversity is seen on day 6 with a secondary peak in diversity on day 16. The lowest diversity is

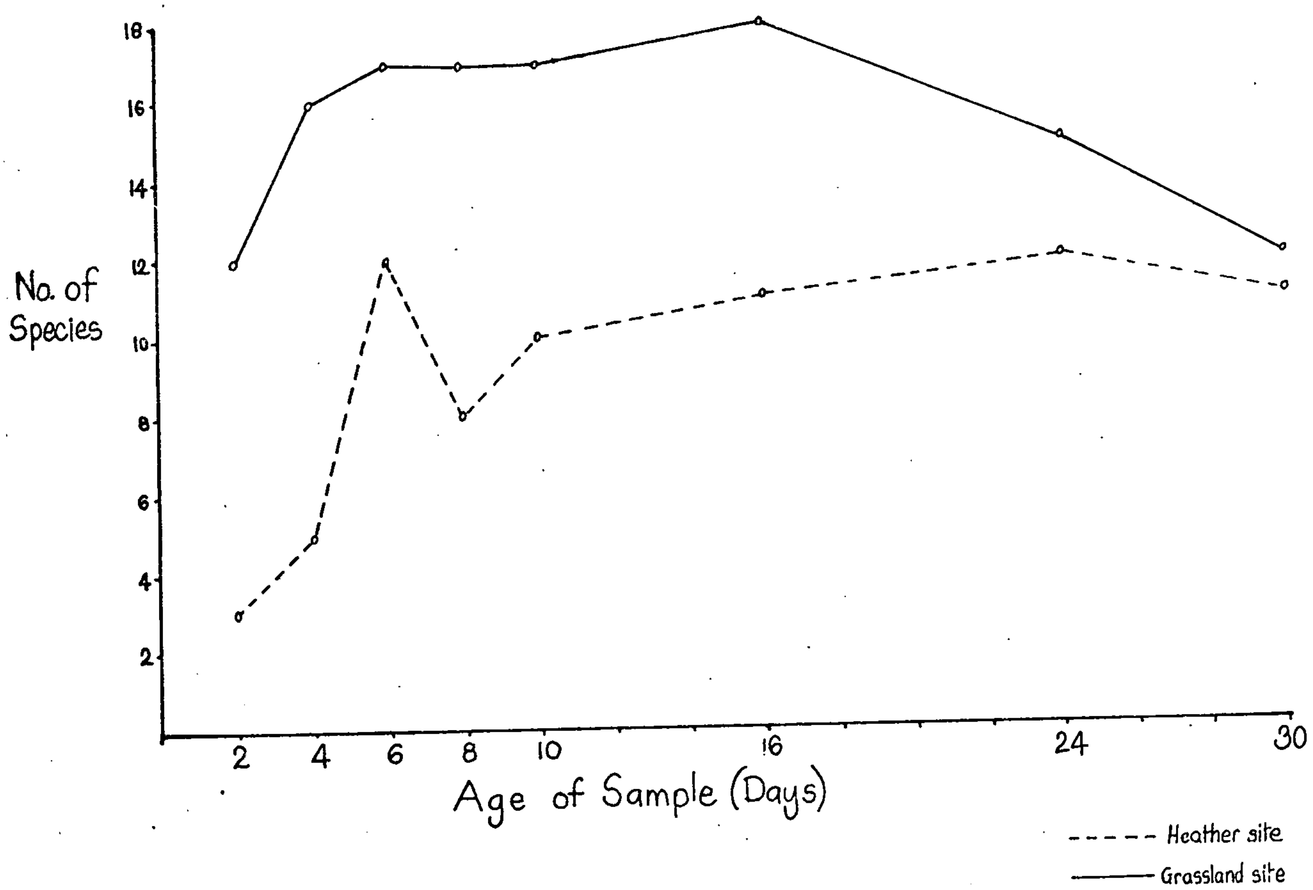


Figure 23 : Number of Species with Age of Dung

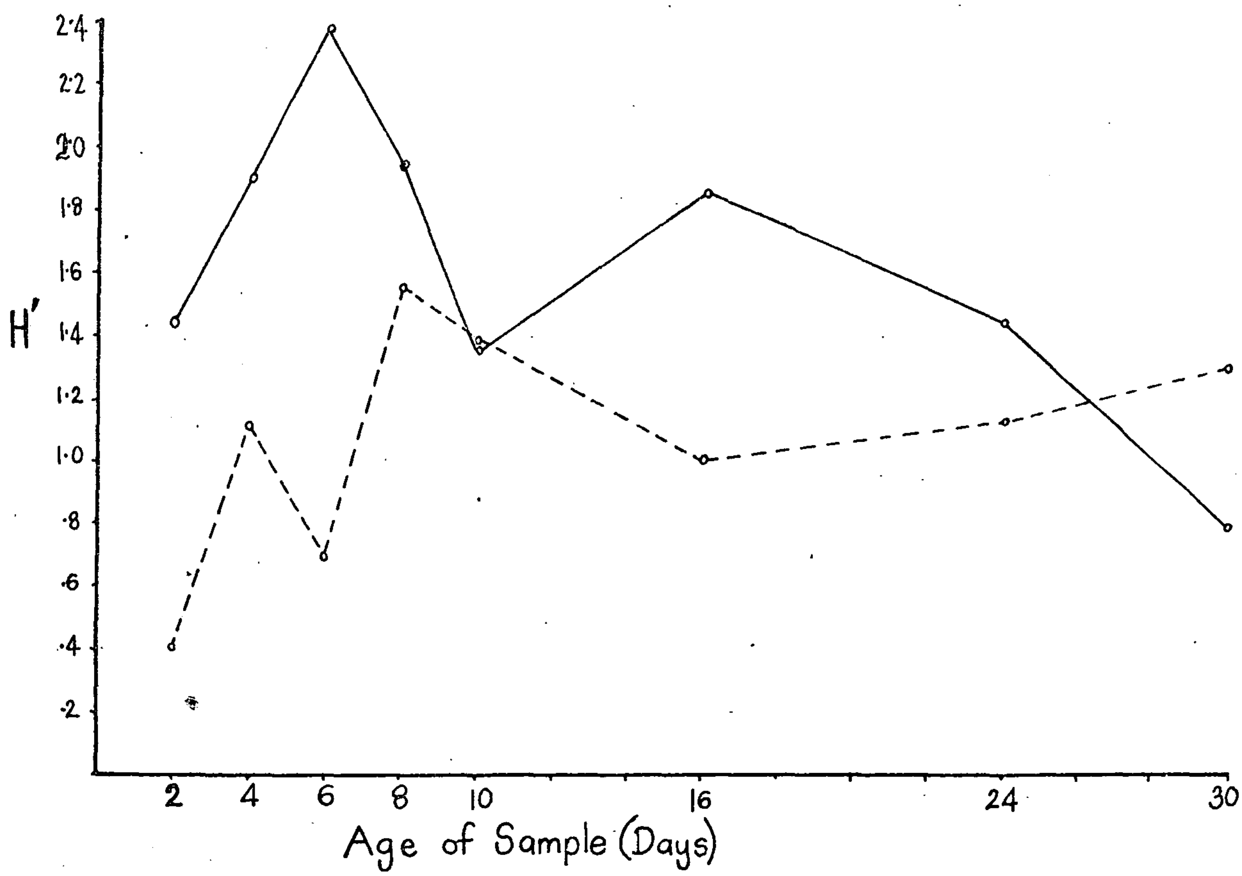
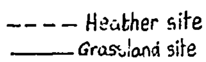
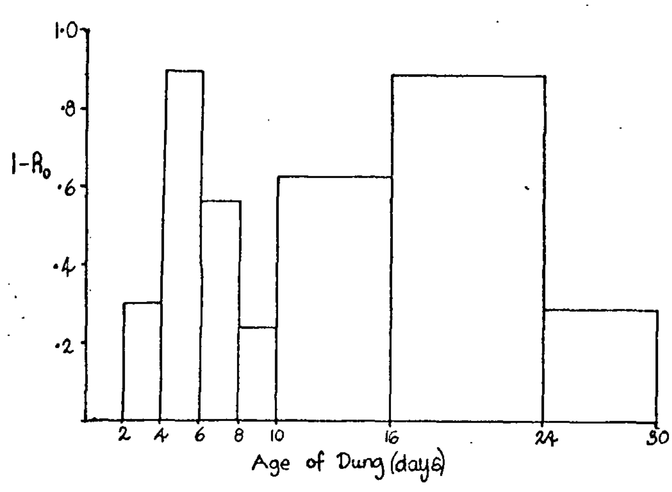
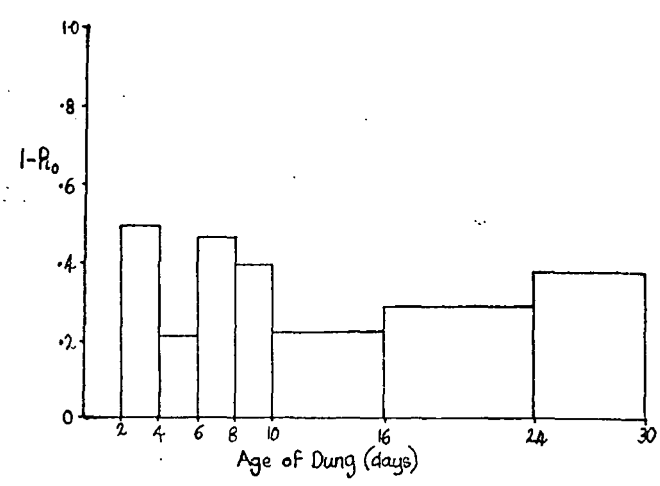


Figure 24 : Diversity (H') with Age of Dung





Grassland site



Heather site

Figure 25 : The Amount of Community Change (1 - R_o) between sampling dates

Table 7: The Number of Species, Individuals, Diversity and Successional Change on the Grassland Site

Day	No. of Species	No. of Individuals	H'	R_0	$1-R_0$
2	12	103	1.4540901	.6716681	.328
4	16	269	1.9007285	.0977463	.9022537
6	17	283	2.3764607	.2417733	.7582267
8	17	234	1.9644945	.7544323	.2455677
10	17	365	1.3609525	.3680978	.6319022
16	18	293	1.861176	.1154388	.8845612
24	15	388	1.4574402	.7005805	.2994195
30	12	370	0.8002286		

Table 8: The Number of Species, Individuals, Diversity and Successional Change on the Heather Site

Day	No. of Species	No. of Individuals	H'	R_0	$1-R_0$
2	3	192	0.4019008	.4981822	.5018178
4	5	163	1.1211857	.7752694	.2247306
6	12	383	0.7002116	.5311107	.4688893
8	8	102	1.558764	.5943917	.4056083
10	10	306	1.3973794	.7702221	.2297779
16	11	589	1.0416053	.7049317	.2950683
24	12	541	1.1665464	.6188161	.3811839
30	11	696	1.3079812		

found on day 30.

Diversity is generally lower on the heather site with the highest diversity seen on day 8.

Amount of Change during Faunal Succession

Although the number of species and the index of diversity show that obvious changes are occuring during the 30 day period, they do not take into account any changes in the species composition of the community.

The following calculations using the Shannon-Wiener index of diversity: H', were carried out for each pair of successive days to give R_O, the amount of overlap between those days (Koskela and Hanski, 1977).

H' was calculated for each day, for example days 2 and 4, to give H'(2) and H'(4). H' was also calculated for each pair of successive days combined to give H'(2 + 4) which was designated as $H'_{observed}$. If the two days contain no species in common, H'(2 + 4) will be maximal:

$$H'_{max} = \frac{H'(2) + H'(4)}{2} + \log. 2$$

If the two days contain the same species in equal proportions, then H'(2 + 4) = H'(2) = H'(4) , which is the minimum value of H'(2 + 4). An estimate of H'_{min} can be calculated:

$$H'_{min} = \frac{N\,H'(2) + M\,H'(4)}{N + M}$$

N = total number of individuals on day 2

M = total number of individuals on day 4

The overlap between days can be calculated as follows:

$$R_O = \frac{H'_{max} - H'_{observed}}{H'_{max} - H'_{min}}$$

1 - Ro represents the amount of change in species composition between the stages.

The results for each pair of days are shown in Tables 8 and 7, and graphically in Figure 25.

On the grassland site the greatest changes in species composition are found between days 4 and 6, 6 and 8 and between days 10 and 16, 16 and 24. Little change and most overlap is seen between days 2 and 4, 8 and 10 and 24 and 30. Thus, there appear to be two main periods of community change; the first during the initial week of dung exposure and the second after about two weeks.

On the heather site, a comparatively large overlap is seen between the communities found on different days. This may be a reflection of the high relative abundance of cyclorrhaphous larvae found on most days on this site.

Fauna extracted from the Soil Cores (Table 9)

Few animals were found in the soil cores. On days 16 and 24, some *Aphodius* larvae were found in the cores under the dung. They may have migrated from the dung to avoid waterlogging conditions. It is known that some species pupate in the soil (e.g. *Aphodius lapponum*), however the larvae found in this case were not in the prepupal stage. There was some evidence of an aggregation of earthworms in the soil beneath the dung samples.

Table 9: Fauna extracted from the soil cores. (Mean number per soil core, with the numbers extracted from control soil cores on each site given in brackets)

Faunal Group

Day	Site	*Aphodius* larvae	Beetle larvae	Hydrophilids	Staphylinids	*Aphodius* adults	Worms	Mites
2	Grass	0	1.8(2.4)	1.1(0)	0	0.7(0)	0.8(0)	3.3(3.6)
	Heather	0	1.3(1.2)	0.2(0)	0.1(0)	0	0.1(0)	1.8(0.8)
4	Grass	0	4.2(-)	1.8(-)	4.6(-)	1.1(-)	0.7(-)	14.4(-)
	Heather	0	1.9(-)	0.7(-)	2.1(-)	0.7(-)	0	5.3(-)
6	Grass	0	1.8(1.8)	0.6(0)	0.5(0.6)	0	0.6(0.4)	7.6(4)
	Heather	0	0.8(1.2)	0.1(0)	0.5(0.4)	0	0.1(0)	2.9(2.6)
8	Grass	1.4(0)	4.2(1.8)	0.3(0)	0.9(0.1)	0.1(0)	0.4(0)	11.9(8.8)
	Heather	0	1.5(0.6)	0.2(0)	0.2(0)	0	0.1(0)	3.4(5.6)
10	Grass	0	2.1(2.6)	0.1(0)	0.1(0)	0	0.5(0.2)	12.0(1.8)
	Heather	0	1.3(1.4)	0	0.5(0.6)	0.1(0)	0.1(0)	4.6(2.6)
16	Grass	2.9(0)	2.4(2.4)	0	0.8(0.8)	0	1.1(0.1)	5.6(3.3)
	Heather	0.2(0)	1.4(2.0)	0	0.3(0.1)	0	0.1(0)	4.4(3.8)
24	Grass	0.8(0)	4.5(1)	0	0.5(0.2)	0	0.2(0.2)	2.4(3.2)
	Heather	0.9(0)	1.3(0.6)	0.2(0)	0.3(0.8)	0	0.1(0)	6.1(2.4)
30	Grass	0	3.3(1.2)	0	0 (0.4)	0	0.1(0.4)	18.1(5.2)
	Heather	.3(0)	1.4(0.4)	0	0.3(0.4)	0	0.1(0)	9.2(7.8)

Discussion

I Succession of Fauna

The succession of fauna found in this study followed essentially the same pattern as that found by other workers. The first colonizers to freshly deposited dung were Cordilurinae flies and other Muscidae and endocoprid dung beetles (Aphodius spp.). The flies come to feed and/or mate and deposit eggs. The dung beetles burrow into the dung, feeding and laying eggs before leaving after a few days. The fly eggs hatch within 3 days but the beetle eggs do not hatch for about 2 weeks.

Hydrophilid and Staphylinid adults arrived at the dung after a few days and stayed for 7-10 days, feeding and laying eggs before flying away. As with the Aphodius adults, they move on to colonize other droppings.

Dipteran larvae and Aphodius larvae were found in large numbers in the dung but showed a separation in their times of maximum abundance. Dipteran larvae reached a peak in the initial stages of dung ageing at 10-16 days and Aphodius larvae are found in greatest numbers after 30 days. Hydrophilid and staphylinid larvae occupied an intermediate position in the succession with the greatest numbers of larvae found after the peak in dipteran larvae but before the peak in Aphodius larvae.

Mites appeared in the droppings after only a few days, some species probably having been carried there by _Aphodius_ adults (_Parasitus_ sp.) or by _Scatophaga_ flies (Gibbons, 1968). They were found in varying numbers for at least 30 days with a turnover in species composition.

The diversity in the coprophagous community increased to a maximum after about one week on both of the sites and another increase in diversity was seen after 16 days on the grassland site.

The amount of change in diversity which included both a change in the species composition of the coprophagous community and a change in the distribution of individuals among these species, also showed two peaks on the grassland site. Initially there was a high rate of change followed by a relatively stable period. Then a more gradual change in the community occured after about 10-24 days, after which little change was seen.

The first, rapid change was probably due to an initial influx of dung-specific coprophages. These feed, grow and reproduce in the dung, some staying for only a few days before searching for new droppings. As the dung ages, it becomes transformed by the macrofaunal community. It becomes more friable as a result of their tunnelling activities and their droppings render the dung even more suitable for microbial decomposition (Breymeyer, 1974; Papp, 1976). There are species changes in the coprophilous fungi (Nicholson, 1967; Denholm-Young, 1969), a decrease in the initially high level of ammonifying bacteria (Jakubczyk, 1974), and possibly changes in the species of bacteria. In addition, rain leaches through and facilitates the disintegration of the dropping.

These changes combine with the fact that the dung has been exposed for a longer period of time, important for the colonization of the more generalist coprophages and saprophages, to produce changes in the faunal community. Therefore, the secondary change in the species comprising the coprophagous community is likely to be due to a gradual influx of generalist saprophages and the soil fauna of the area. This is supported by the trophic status of some of the fauna found in the later stages; lumbricid worms, slugs, ptiliid beetles, mycetophilid, chironomid, cecidiomyiid and psychodid larvae and certain mites which form part of the soil fauna.

The change in the coprophagous community during the latter stages of dung ageing is also partly accounted for by the replacement of beetle adults by beetle larvae. In the community analysis, the two different stages in the life-history were considered as separate 'species' due to their differences in feeding habits. For example, hydrophilid adults are coprophagous whereas the larvae are carnivorous (Imms, 1960). Aphodius adults and larvae also differ in their feeding specializations as outlined in Section III.

On the heather site, the diversity was found to be lower and fewer species were encountered. There was relatively little change in community composition during the sampling period. This was probably due in part to the paucity of soil fauna under the heather, which was clear from the soil cores extracted. This, in conjunction with the greater height of the vegetation which may impede dung location by olfactory mechanisms, did not facilitate colonization by generalist saprophages.

II Comparisons with Other Studies

The differences found in the faunal composition and succession between this study and previous studies can be subsumed under two main headings.

1) A delay in, and the prolonging of, successional stages.

This was especially obvious in the case of Diptera. In the present study, the dung appeared suitable for oviposition for a longer period of time and 'primary' fly larvae showed a considerable overlap with 'secondary' fly larvae (Papp, 1976, refer to Section III). Olechowicz (1974), investigated succession on sheep dung and found that the numbers of fly larvae were maximal in the first 5 days and decreased after 10 days. In the present study, fly larvae showed a peak in numbers in the 10-16 day period.

The differences between the findings of the present study and other studies are probably attributable to the colder, wetter conditions at Muggleswick. Thus, the dung remains moist for a longer period and microbial decomposition is slower. In addition, the development of larvae is prolonged at lower temperatures (Gibbons, 1968; Laurence, 1954).

2) A relative paucity of species.

This may be due to an interaction of several factors.

(i) The sampling period only covered one month of the year, in contrast with other studies (Laurence, 1954; Mohr, 1943; Olechowicz, 1974). Thus, certain arthropods showing seasonal variation in numbers will not have been sampled. For example, preliminary observations in May, 1980, on dung fauna, found several specimens of Aphodius sphacelatus (Panzer). This is a species commonest early in the year (White, 1957) and only one individual was found during the present sampling period.

(ii) Most other studies have investigated the fauna living in cow droppings, which are far larger than sheep droppings (about 2kg) and present a larger surface area. With respect to the dung-inhabiting fauna, droppings can be regarded as discrete units separated by generally non-productive areas, ie islands. It is known (MacArthur and Wilson, 1967) that smaller islands have fewer species than larger islands and this phenomenon, found among a variety of taxonomic groups, may also apply to the dung fauna.

(iii) Sheep are known to have less thorough digestive systems than those of ruminants, thus, sheep dung may contain a higher proportion of raw fibre and a lower microbial population. This may influence colonization by certain species.

(iv) Most extensive investigations of dung fauna have concentrated on lowland areas, or areas with a relatively mild climate. The number of invertebrate species found in upland areas is sparse compared with lowland Britain (Coulson and Whittaker, 1978) and this may partly explain the dearth of species found.

The lack of predator species: fly larvae, Histeridae beetles and Sphaeridium beetle larvae may be associated with the colder, wetter climatic conditions combined with increased searching activity necessary in an area having a relatively low density of suitable habitats.

The paucity of species and number of individuals, combined with their slower rate of development, may have been factors in producing the low percentage of organic matter lost through the 30 day sampling period, 1 - 1.5%, as compared with Holter's (1979) finding of a 20 - 25% loss in 11 - 14 days in cow dung.

III Trophic Relationships within Droppings

The most numerous coprophages found are hydrophilid and *Aphodius* adults, fly larvae and *Aphodius* larvae and these groups show differences in their feeding specializations.

Aphodius adults have narrow channels in their mandibles and require more fluid feeding material, whereas the larvae have strongly sclerotized mandibles enabling the consumption of coarser substratum and are also able to digest bacterial albumens, a vital qualification for subsistence in old droppings (Landin, 1961).

The dipteran larvae were classified by Papp (1976) into 'primary' and 'secondary' larvae found in earlier and later stages of dung ageing. Primary larvae (Muscidae, Sepsidae) have intestine lengths exceeding their body length, a strongly reduced cephalo-pharyngeal skeleton and consume semi-liquid material - the easily decomposing 'cementing' substances in the dung. The secondary larvae have shorter intestines and possess oral organs suitable also for the gnawing of harder substances and can feed on undecomposed plant remains. The latter, mainly Nematocera, are thus specialized for existence on older dung.

There are probably further specialisations within the coprophagous groups. For example, Mycetophilid larvae generally have a dominance of fungi in their diet and the larvae of the staphylinid beetle, Megarthrus depressus (Pk), eat the spores of fungi (Kemner, 1925). However, as yet the feeding biology of most Diptera and Coleoptera is too imperfectly known to enable their allocation to a particular successional stage based on their feeding requirements.

In the latter stages of dung ageing, lumbicids are usually important in the removal of dung (White, 1957). As well as ingesting particles of dung, many species also ingest large quantities of mineral soil (Edwards and Lofty, 1972). This accelerates the process of decomposition due to intestinal microflora and combines the organic matter with the soil. In this study, earthworms were found in low numbers after 16 days on the grassland area, with some evidence of aggregation in the soil underneath the dung. Even lower numbers were retrieved from dung on the heather site.

The predators in the dung community of this study were staphylinid beetles, mites and hydrophilid beetle larvae. Only one specimen of the hydrophilid beetle Sphaeridium was found. The larvae of this genus are carnivorous and in certain situations constitute one of the most important mortality factors in dipteran larval populations (Hammer, 1941).

Similarly, bearing in mind the difficulty of larval identification, no predatory dipteran larvae were found, although predatory Mesembrina larvae were found during the course of a preliminary study. This is in contrast with other studies where carnivorous fly larvae are important predators.

The most numerous predators in this investigation were certain staphylinid adults and larvae, which prey largely on dipteran eggs, larvae and pupae, mites and other Staphylinidae (Mank, 1923). Staphylinid beetles can account for a large proportion of fly mortality in some dung communities - Valiela (1969)b suggested that they could have caused a reduction in fly populations of 45 - 51%.

Little is known of the details of the feeding preferences of various staphylinid species, although this may be a major factor in determining their presence at a particular successional stage. For example, Tachinus rufipes (De. G.) was generally seen in the initial stages of dung ageing and probably feeds on dipteran eggs.

The numbers of staphylinid adults were higher on the grassland site and the numbers of dipteran larvae, their most probable food source were higher on the heather site. This could be due to two factors. Firstly, the higher vegetation on the heather site could, by impeding the air flow, make the dung more difficult to find. Secondly, the different numbers of Aphodius beetles on the two sites could have an effect on the availability of dipteran larvae to staphylinid beetles. Aphodius adults create tunnels through the dung enabling the staphylinids, which lack fossorial adaptations, to utilise these tunnels to feed upon otherwise unavailable larvae (Hammer, 1941). The feasability of this interaction was demonstrated experimentally (Valiela, 1969) and is supported in this study where fewer _Aphodius_ beetles colonised samples on the heather site and fewer staphylinids were found on this site. In addition, these samples appeared subjectively to be less riddled with _Aphodius_ tunnels than the samples from the grassland site.

The other group of predators were mites. Macrochelid mites are known to feed on muscid eggs (Rodriquez and Ibarra, 1967) and mites of the genus _Parasitus_ attach themselves to thin-cuticled areas of _Aphodius_ beetles and suck the body fluids (White, 1957). The proportion of predatory mites in this study is not known.

Occasional predatory Carabid beetle larvae were found in the samples (_Trichocellus cognatus_, _Calathus_ sp.) and several elaterid larvae (_Athous_ sp.). The latter are not generally regarded as predatory, however, they may be obligate carnivores, as individuals kept in petri dishes were seen to eat dipteran pupae and they have been observed holding crushed _Aphodius_ adults and larvae (White, 1957).

IV Can dung-inhabiting Fauna be considered as a Community?

A community can be defined as an assemblage of populations of living organisms in a prescribed area or habitat (Krebs, 1978). The anthropod species associated with herbivore droppings constitute a characteristic assemblage peculiar to this situation. The collection of populations associated with the relatively well-defined and discrete habitat of a dropping can be regarded as a community.

The same groups of species recur in space and time and analysis of their relative abundance, diversity and trophic structure gives results that are biologically meaningful and provide information on the degree of variability and interaction between discrete dung communities.

However, species differ in the degree to which they are associated with the dung habitat. Scatophaga flies, for example, lay eggs in dung but the adults are predatory, feeding on flies that may or may not be associated with dung (Gibbons, 1968). Females of the Muscid Fannia may use the dung as food and oviposit in dung but also in other situations containing high concentrations of organic matter. Many of the carnivores found in the dung community have a variety of other microhabitats available to them (Koskela and Hanski, 1977). Thus, species found in the dung community may also be part of wider communities.

The species assemblage comprising the community may vary according to various factors, for example, season, macrohabitat, microclimate. There are probably several dung communities showing overlap and varying according to various factors which are considered in Section VI. It is possible, however, that although the species comprising the community may differ, the relative biomass of individuals within a particular ecological group may show less variation.

Further investigations must be carried out on the biology of the species inhabiting herbivore dung before such analyses can be carried out. The simple division into coprophages and carnivores that is possible at present obscures the presence of possibly important subdivisions as well as those species of omnivorous status.

V Factors influencing Dung Disappearance

This study found that the losses of dry matter and organic matter were relatively low during the 30 day period. However, despite the prolongation of decomposition, the relative contribution of fauna to this process may be important. On the grassland site, several groups of invertebrates were found in high proportions, with worms probably increasing in importance later in the stages of dung ageing. Aphodius adults were found in most samples, and their burrowing activities accelerated the disintegration and weathering of the dung.

On the heather site, the dipteran larvae were numerically the most important group and, given the low numbers of predators, their survival rate is likely to be fairly high, resulting in a relatively high proportion of the dung being exported upon their emergence from pupation.

On the grassland site, growth of vegetation during the period under investigation played a part in the breaking up of the dung samples. On the heather areas, as most dung is deposited on the sheep paths, trampling by sheep is probably an important factor in its disappearance, although through rendering the dung unsuitable for faunal colonisation, it may decrease their relative contribution to the process of decomposition.

VI Factors affecting the presence and abundance of species living in dung

The information provided by this study can be combined with other studies to give an outline of the factors affecting the composition of the dung community. As will be clear from the discussion below, these factors are not discrete in their action but interact to a greater or lesser extent and their action varies with the species concerned.

(i) Geographic situation

The species inhabiting herbivore dung may vary in different parts of the world, not only in connection with climatic changes, but also with the different types of herbivorous animals found. Thus, Australia has a dung-inhabiting fauna adapted to pellet-like marsupial droppings rather than large, moist ungulate droppings (Bournemissza and Williams, 1970).

(ii) Macrohabitat, Microclimate, Season and Weather

These factors generally affect fauna through the action of moisture, temperature and dispersal.

Most species show a predictable and seasonal variation in their abundance at least in temperate climates and in the case of dung fauna, this is probably the result of climatic factors or possibly competitive exclusion by species of similar ecological status rather than the availability of food.

The macrohabitat can have a clear effect on the community (e.g. Koskela and Hanski, 1977). In the aforementioned study, dung was placed in three different habitats; pine and spruce forest and grassland. These had different densities of dung already present on the site from grazing domestic or wild herbivores. As the level of background dung is important in determining faunal colonization, the extent to which this was a factor in determining the dung community found in this study is not clear. In the present study, the two habitat sites were not far displaced from each other. Therefore, the density of dung in the respective areas is probably not an important factor in determination of the communities found. The difference in fauna on the grassland and heather areas is probably due to the effects of the microclimate. Under the heather, temperatures are generally cooler and humidities higher, with less variation in both than on more exposed sites (Delany, 1953). In addition, the height of the vegetation on the heather site probably resulted in the impairment of dung location by beetles although it appeared not to disrupt the location mechanisms of flies. This is supported by the investigations of White (1960b), on North Penine moorland, whose data show that the percentage of droppings infested by _Aphodius_ beetles was higher on the grassland areas. Similarly, his data show a higher infestation percentage of Diptera on the heather sites due probably to the more moist microclimate prolonging suitable oviposition conditions.

General climatic factors influence the dung community through the action of moisture in the dung and temperature. The present study showed a delay in the rate of succession compared with other lowland studies and this is probably due to the higher rainfall and lower temperatures in upland conditions. A monthly average of 157 mm of rain has been recorded at Moorhouse National Nature Reserve in the North Penines which is at a higher altitude than Muggleswick (Heal and Smith, 1978). If the weather is warm and dry, there is an increased rate of moisture loss from the dung. Landin (1961), working on a lowland area in Sweden, found a moisture decrease from 80% to 11.5% in three days under torrid conditions, which eliminated the dung fauna.

Gibson (quoted in Denholm-Young, 1969) found that at lower altitudes in the Sierra Nevada of British Colombia, dung disappeared rapidly through the action of beetles, but at high altitudes the disappearance was slow, possibly due to the night temperatures being too low for the survival and breeding of beetles.

(iii) Type of Herbivore

Dung produced by different herbivores has passed through different kinds of digestive system which leads to variation in the degree of breakdown of plant material and the type and amount of intestinal micro-flora and fauna. Herbivores generally differ in their selectivity of the vegetation eaten, which affects the dung both chemically and physically. The degree to which these differences affect the dung community is not known. Castle and MacDaeid (1972) treated herbage with high or low levels of nitrogen to investigate the effect on the decomposition of pats produced by cows feeding on the treated areas. No difference in decomposition rate was seen although both levels of nitrogen were probably too high to show a differential effect.

It is difficult to separate the influence of specific dung dry weight composition from factors such as the size of droppings and the amount of moisture which also vary between herbivores and which are known to have an independent influence on faunal colonisation (White, 1957; Landin, 1961).

(iv) Age of Dung

The age of the dung has a marked influence on the community as shown in this and other studies (e.g. Laurence, 1954; Papp, 1976). Laurence suggested that dung age may influence invertebrate succession through fungal and bacterial succession but decided that the amount of moisture might be more important. The present study found relatively little change in moisture, although a definite succession in the community was seen. The time of dung exposure probably affects the faunal component, although this is difficult to separate from other changes that occur during ageing.

A characteristic fungal succession can be found in dung (Denholm-Young, 1969) although bacterial changes have received little attention. It is hypothesised that the main factor influencing the appearence of different species during dung ageing may be the presence and type of macrofauna and microflora and fauna , which results in a 'facilitation' type of succession (Connell and Slatyer, 1977).

(v) The Distribution of Droppings

The migration of fauna between droppings and the effect on the fauna of different dung distributions has received little attention to date.

The dung-producing herbivores in most investigations have been components of highly managed and usually intensively grazed systems. The area used in the present study differs to a certain degree in that the sheep are found in low densities on a relatively 'natural' habitat and their grazing of different areas is not controlled. This has a marked effect on the distribution of dung (White, 1960b) and presumably also on the fauna colonizing it.

VII Suggestions for further Investigations

The fauna colonizing dung provide a rapidly changing situation that is easy to manipulate enabling determination of the variables affecting the community. Dung provides an ideal habitat for a variety of community studies, for example; predator-prey relationships, the transfer of energy through the community, the trophic relationships in different kinds of dung, etc. In addition to sheep, Muggleswick Common also has some cows and horses grazing in a relatively uncontrolled manner. This provides an interesting situation for the comparitive study of faunal communities inhabiting the dung of different herbivores in the same general habitat. Investigations on the distributions of droppings and their associated faunal communities might provide an insight into the dispersal and migration of various components of that community.

The faunal influence on the decomposition of dung has been neglected in most British agricultural studies of nutrient cycling (e.g. Floate, 1970). In upland conditions in particular, where nutrient levels can limit the amount of primary production, a detailed knowledge of the dung faunal populations and the variables affecting them is needed.

Summary

1. 160 reconstructed sheep dung pellets were placed on two moorland sites dominated either by heather or by grass, on a single day.
2. Pellets were collected after 2, 4, 6, 8, 10, 16, 24 and 30 days. 10 pellets were taken from each site on each sampling day.
3. The fauna was extracted from the dung samples collected. The faunal groups investigated were Acarina, Coleoptera and Diptera larvae.
4. A succession in the species composition and relative abundance of faunal groups was found with age of dung.
5. Faunal succession was found to be more rapid on the grassland site than on the heather site.

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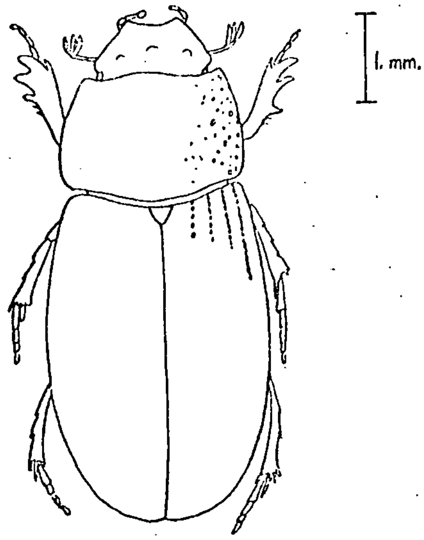
Appendix I

Numbers of Individuals of the Species found with Dung Age (Numbers from the Heather Site in Brackets)

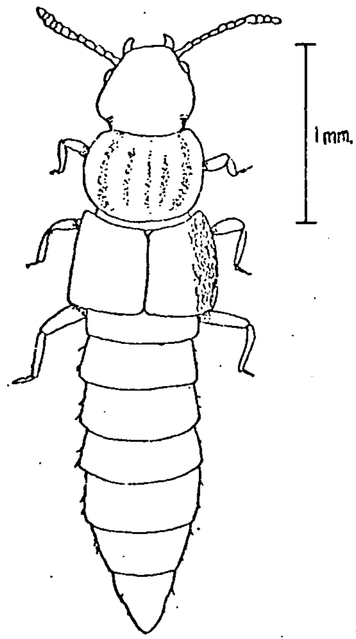
			DAY 2	4	6	8	10	16	24	30
COLEOPTERA										
Carabidae										
	Larvae	Calathus sp.						1		
		Trichocellus sp.		(1)						(1)
Elateridae										
	Larvae	Athous sp.						6	3 (1)	1
Hydrophilidae										
	Adults	Cercyon atomarius (Fabr.)	4	19	23 (1)		1			
		Cercyon haemorrhoidalis (Fabr.)	1	3						
		Cercyon lugubris (Olivier)			5		3			
		Megasternum obscurum (Marsh.)	4 (2)	17 (2)	39 (4)	35 (10)	63 (30)	25 (18)	5 (2)	(7)
		Sphaeridium sp.			1					
	Larvae	Cercyon spp.				2	15 (1)	69 (2)	58 (9)	25 (15
Ptiliidae										
	Adults	Ptenidium sp.						(2)	4 (1)	2
Scarabaeidae										
	Adults	Aphodius ater (Degeer)	1	17 (5)	16 (6)	36 (20)	17 (9)	5 (5)	2	
		Aphodius depressus (Kugel.)	1	4	7	2				
		Aphodius fasciatus (Olivier)	1	2		2 (1)	(1)			
		Aphodius fimetarius (Linn.)			1		1			
		Aphodius lapponum (Gyll.)	43 (21)	34 (18)	41 (18)	15 (41)	1 (24)		1	
		Aphodius luridus (Fabr.)			1					
		Aphodius rufipes (Linn.)			(1)	(1)	1			
		Aphodius sphacelatus (Pauzer)		1						
	Larvae	Aphodius spp.						30 (1)	253 (40)	245 (334)
Staphylinidae										
	Adults	Dimetrota atramentaria (Gyll.)			7 (5)	32 (11)	61 (24)	27 (1)	(4)	(2)
		Megarthrus depressus (PK)		10	12 (1)	1	2			
		Oxypoda sp.				(2)	23 (2)	4	1	
		Oxytelus laqueatus (Marsh.)	4	5	29 (1)	5	3 (1)			
		Tachinus rufipes (De G.)	(3)	2	4 (5)		6	(1)		
		Unidentified species	17	16	16 (8)	27	12 (7)	5	(4)	(1)
	Larvae	Aleocharinae				15 (4)	54 (15)	51 (9)	8 (3)	4 (6)
		Megarthrus sp.						9	5	2 (16)
		Oxytelus sp.					1	22 (2)	37 (6)	1 (2)
		Tachinus sp.							2	3
		Unidentified species						1	6	
DIPTERA										
	Larvae	Borboridae (incl. Borborus flavipennis (Haliday), Sphaerocera subsultans (Linné), Leptocera sp.)		128 (58)	(23)	97 (21)	230 (128)	121 (377)	45 (204)	16 (229
		Scatophagidae, Anthomyiidae (incl. Chortophila sp., Scatophaga stercoraria (Linn.), Scatophaga furcata (Say.)).	30 (169)	16 (80)	104 (323)	6 (7)	27 (107)	1 (143)	(269)	(67)
		Fannia sp.						1	(3)	(2)
Nematocera										
		Cecidiomyidae							15	15
		Chironomidae		2			(3)	3 (1)	(5)	3
		Mycetophilidae						1		
		Psychodidae						53 (37)	(3)	1 (14)
		Tipulidae								
		Tipula subnodicornis (Zett.)		(3)						
ACARINA			(3)	42 (6)	48 (18)	90 (29)	92 (28)	52 (17)	22 (12)	33 (35)
ANNELIDA										
		Bimastos eiseni (Levinsen)			(1)			4 (1)	5 (2)	5
GASTROPODA										
		Slug	1					4	(2)	2 (2)

Appendix 2

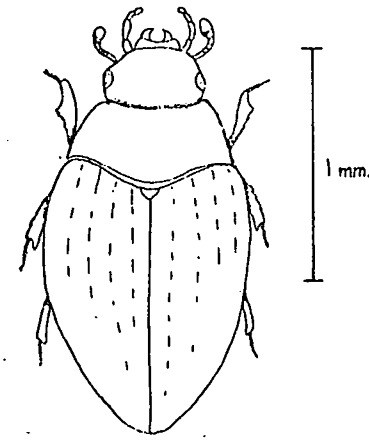


Scarabaeidae :

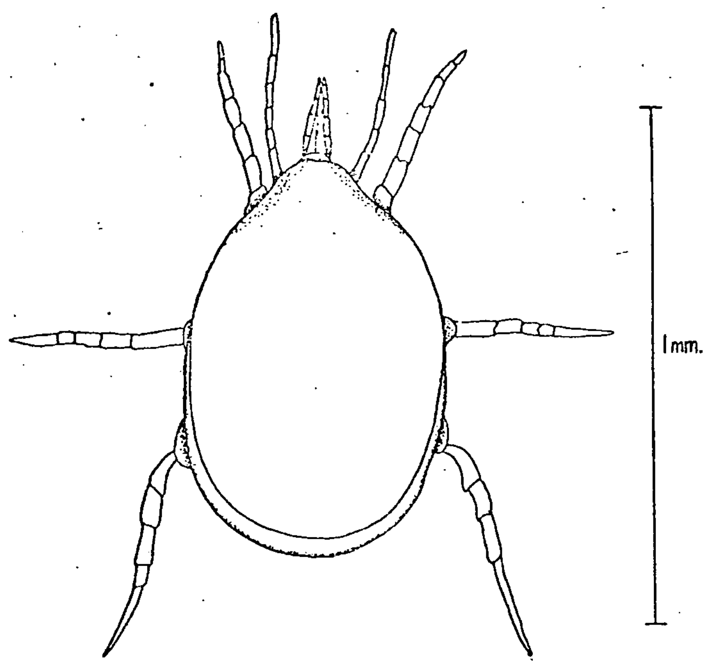
Aphodius lapponum
(adult)



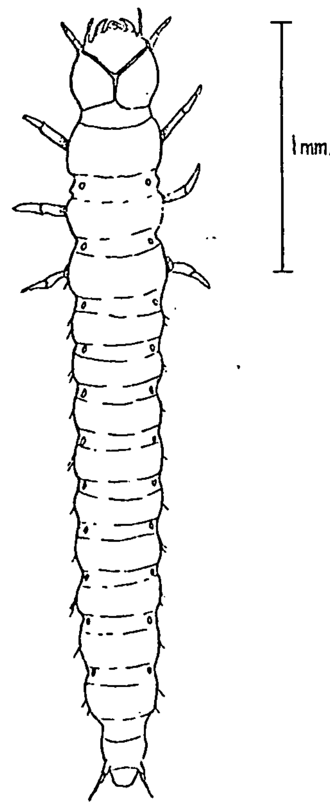
Staphylinidae : Oxytelus laqueatus
(adult)



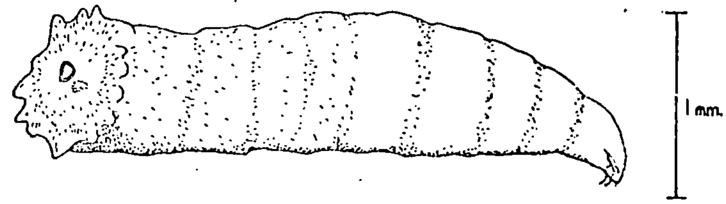
Hydrophilidae :
Megasternum obscurum
(adult)



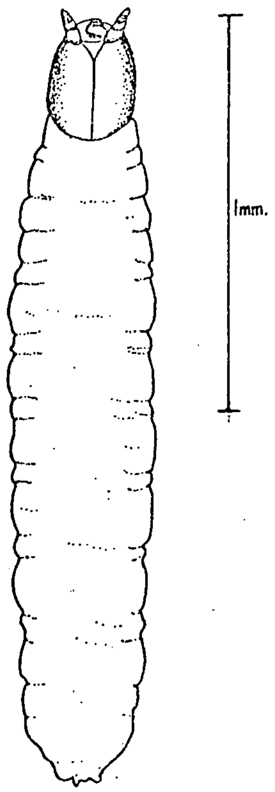
Acarina : Unidentified Species



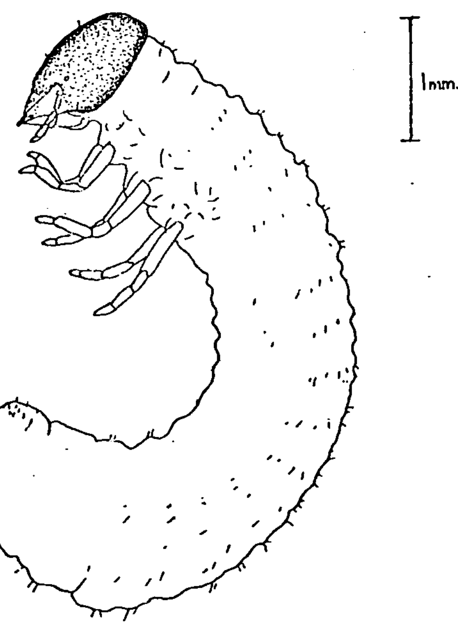
Staphylinidae : Oxytelus sp.
(larva)



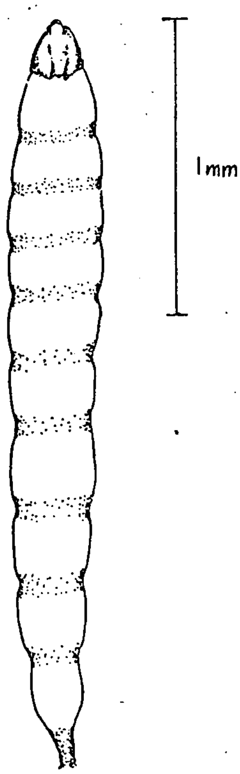
Diptera : Scatophaga sp.
(larva)



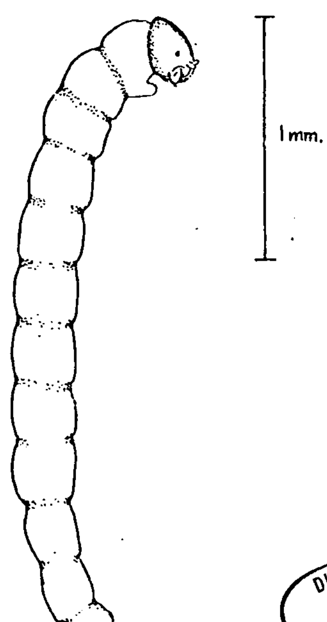
Hydrophilidae : Cercyon sp.
(larva)



Scarabaeidae : Aphodius sp.
(larva)



Psychodidae : larva



Chironomidae : larva